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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 76, NO. 5, PP. 319–336 SEPTEMBER, 1949

DIFFERENTIAL CHROMOSOME SEGMENTS IN TRILLIUM ERECTUM L.[1]

PAUL C. BAILEY

In recent years there have appeared numerous papers in the field of cytotaxonomy which have been concerned with the cytological aspects of certain species of *Trillium*. A number of papers have attempted to establish differences between closely related species on the basis of visible differences in their chromosome morphology, the usual criteria of difference being the total length of the chromosomes and the relative length of the chromosome arms.

Haga (1934) concluded from his studies of *Trillium kamstchaticum*, *Trillium smallii* and *Trillium tschonoskii* that, "it is hardly tenable to consider the slight differences in length and form per cents in absolute lengths of the chromosomes found between different species as being significant". Barksdale (1938), as a result of his studies of the pedicellate species of *Trillium* from the southern Appalachians, states "that such an attitude, which seems to result from the assumption that such minor floral and vegetative variations peculiar to any one species will be reflected in the morphology of one or several of the chromosomes of the species complement, is, at least, in the case of *Trillium*, a rather naive one."

If one accepts the conclusions of Haga (1934) and Barksdale (1938), it is then necessary to employ other criteria in order to find cytological differences which may exist between closely related species of the same group.

From time to time there have appeared in the literature accounts of experimental treatment that rendered visible linear differentiations in the chromosomes not otherwise observable. Shmargon (1938) observed these regions in *Secale cereale*, Darlington and LaCour (1938, 1940) in *Paris* and *Trillium* species, Wilson and Boothroyd (1941, 1944) in *Trillium* species and *Secale cereale* and Kakhidze (1938) in *Crepis capillaris*. In animals they have been found by Callan (1924) in *Triton* species. These differentiations have taken the form of regions of reduced diameter and staining capacity, sometimes so numerous as to give the chromosomes a chromomeric appearance. The differentiated regions may be of varying length, and may appear within or at the end of the chromosome arms.

[1] Portion of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Vanderbilt University, Nashville, Tennessee.

[THE BULLETIN for July–August (76: 235–318) was issued July 1, 1949]

The investigations summarized above indicate that such differentiated regions were produced in the somatic chromosomes of a variety of plants. Darlington and LaCour (1938, 1940) produced regions of reduced diameter, highly specific as to locality, in mitotic metaphase and anaphase chromosomes of *Paris* and *Trillium* by cold treatment for several days; they called this phenomenon "differential reactivity." This term, as used by Darlington and LaCour (1938, 1940), describes a condition entirely similar to the regions of reduced diameter and staining capacity reported by the other cited investigators. The same effect was obtained by Kagawa (1929) and Ellenhorn (1935) by treatment of *Triticum* root tips with chloral hydrate.

In Arctic species of several of the grasses Flovik (1936) found an exceptionally high number of secondary constrictions in most individuals he investigated. In some cases these were so numerous that the chromosomes had a beaded appearance. It appears to the writer that the effective agent in this case may possibly be the constant low temperature in such an environment.

Although experimental proof is not yet available, all the phenomena described above may probably be considered as differential reactivity of chromosomes. Inasmuch as such differential reactivity almost certainly indicates a basic and inherent differential pattern in the chromosomes, knowledge concerning the origin and behavior of such regions is of considerable importance in the understanding of chromosome structure and behavior.

There are many aspects from which differential reactivity might be investigated, chemical methods being especially desirable. Before the latter are undertaken, however, a purely cytological investigation is indicated. Such an approach has been made both by Darlington and LaCour (1938, 1940) and by Wilson and Boothroyd (1941, 1944).

As described by Darlington and LaCour (1940) exposure to cold for a sufficient length of time prevents certain regions of the metaphase and anaphase chromosomes of *Trillium* from staining normally. As a rule these regions were understained, and measured only about one half the diameter of the unaffected portions of the chromosome. Rare exceptions to this were observed in some regions understained but not of reduced diameter, as well as narrower regions which were not understained. The length of constictions varied, the terminal ones being somewhat longer. Most constrictions occurred in the proximal third of the chromosome arm, but in one chromosome constrictions occurred in the distal third.

According to these same investigators, although the size of the differential segment is subject to some variation, its position is constant and

specific. Each chromosome has a characteristic pattern of differential reactivity, some regions being apparently more readily affected than others, especially the terminal ones.

Wilson and Boothroyd (1941) also devoted attention to the rate with which differential segments appeared. They exposed root tips of *Trillium erectum* L. to 3° C. for periods of from 15 minutes to four weeks. Differential regions appeared after 30 minutes, and after exposure for 96 hours nearly all chromosomes were affected. These investigators concluded that in *Trillium erectum* L. maximum differential reactivity had been reached by 96 hours of cold treatment. Although they considered their work on recovery rate somewhat inadequate, they found the time for recovery to be much shorter than that required for the differential segments to appear. After 90 hours exposure to cold the chromosomes returned to normal in about 10 hours at room temperature, most of the recovery occurring in 4 or 5 hours. The relatively rapid rate of recovery is not unexpected, however, inasmuch as the rate of mitosis must also be increased at room temperature.

Darlington and LaCour (1940) believe that differentiated segments produced by cold are the results of nucleic acid starvation. They state that, ". . . in *Trillium*, nucleic acid starvation requires three days to affect the metaphase of mitosis in the roots. Even at a low temperature this period must comprise most of the resting stage. The starvation effect therefore acts long before the prophase when the chromosomes are actually taking up nucleic acid." This is in sharp contrast to the observations of Wilson and Boothroyd who observed the beginnings of differentiation after only half an hour at 3° C. Darlington and LaCour (1940) also state that the differentiated segments represent the heterochromatic regions of the chromosomes, and identify them with the chromocenters of the resting nucleus.

Wilson and Boothroyd (1944) are of the opinion, "that the differential staining capacity of the various parts of the chromosomes under the stimulus of cold is essentially due to a difference in their contraction, which is a manifestation of differential coiling." This they say, "may or may not be causally related to an upset in the nucleic acid metabolism."

Darlington and LaCour (1940) have illustrated a number of homologous pairs of chromosomes that differ in number, size, or position of the differential segments, or in various combinations of these. They designated such pairs as hybrids, but Wilson and Boothroyd (1944) prefer to call them heterogeneous pairs because the term implies genetic hybridity. They also point out that even this assumption may not be justified, inasmuch as one cannot be certain that differential reactivity has not reached

a point of stability, and even when this is reached, it is not clear how long stability lasts.

With regard to the length of the cold-treated chromosomes Darlington and LaCour (1940) report that, "certain segments in each chromosome are reduced to half the standard diameter of the chromatid and appear understained from late prophase until anaphase. They remain their usual length." They also state that, "the heterochromatic segments are the same length when under-charged as when normally charged." The term "charged" as used by Darlington and LaCour (1940) here refers to the charging and under-charging of the chromosomes with nucleic acid.

Wilson and Boothroyd (1944) have observed differentiations of the chromosomes from late prophase until telophase, "during which time their contraction is greatest." With regard to the length of the chromosomes during cold treatment they observe that, "low temperatures cause greater than normal mitotic contraction of the chromosomes" and that, "there is clear evidence of related differential reactions of chromosome segments in both stainability and contraction following a period of cold treatment." These investigators measured the length of the normal chromosome complement as well as that following cold treatment. They found that the total length of the chromosome set (2n) was reduced from 285 ± 6.9 microns, the length of the normal complement, to 234 ± 4.5 microns after 96 hours at 3° C.

Darlington and LaCour (1940) suggest that differential reactivity may be used as a genetic and taxonomic indicator, a criterion of variation between species. It was the primary purpose of the present study to determine whether there exists any such variation between the Canadian *Trillium erectum* L. studied by Wilson and Boothroyd (1941, 1944) and the same species as found in the southeastern United States. If differential reactivity is a constant, specifically recurring phenomenon, the Canadian and Tennessee plants of *Trillium erectum* L. should exhibit the same pattern in response to low temperature treatment.

Material and Methods. A total of approximately 300 rhizomes of *Trillium erectum* L. were collected at the foot of the Cumberland escarpment near Sparta, Tennessee. Some were planted in a bed out-of-doors and others were potted in the greenhouse. An abundance of fresh growing tips was available almost continually. Cold treatment was provided with a commercial electric refrigerator which maintained a fairly constant cold temperature at 3° C. The cold-treated root tips were secured from rhizomes which had been placed in peat moss before transfer to the refrigerator.

Most material for study was prepared using the Feulgen technique together with a squash method. A detailed account of the procedure is sum-

TABLE 1. *Comparative data on chromosome morphology of T. erectum L. and T. luteum (Muhl.) Harbison*

Material	Chromosome A			Chromosome B			Chromosome C			Chromosome D			Chromosome E			Total
	L.A.	S.A.	T.L.	L.A.	S.A.	T.L.	L.A.	S.A.	T.L.	L.A.	S.A.	T.L.	L.A.	S.A.	T.L.	Length
1. *T. erectum*																
Fuelgen Tech.	15.6	1.7	17.3	15.0	4.7	19.7	9.3	5.1	16.4	12.3	8.3	20.6	14.2	13.5	27.7	199.4
2. *T. erectum*																
Feulgen Tech.	16.1	1.1	17.2	13.0	5.9	18.9	8.7	5.4	14.1	9.9	6.3	15.2	14.1	12.7	26.8	186.4
3. *T. erectum*																
Aceto-carm.	.....	....	22.3	20.7	8.4	29.1	12.2	9.5	21.7	16.1	12.2	28.3	20.1	20.1	40.2	285.0 ± 6.9
4. *T. erectum*																
Aceto-carm.	.....	....	18.7	16.4	8.5	24.9	9.4	9.4	18.8	13.0	10.0	23.0	15.8	15.8	31.6	234.0 ± 4.5
5. *T. erectum*																
Aceto-carm.	20.2	1.5	21.7	16.8	11.7	28.5	10.5	8.5	19.0	14.2	9.1	23.3	20.7	19.8	40.5	266.0
6. *T. erectum*																
Aceto-carm.	13.6	1.5	15.1	13.3	7.5	20.8	8.4	6.2	14.6	14.0	7.6	21.6	14.7	13.8	28.5	201.2
7. *T. luteum*																
Aceto-carm.	19.8	1.5	21.3	15.3	11.0	26.3	13.3	10.3	23.6	19.1	6.7	25.8	21.0	18.7	39.7	273.4
8. *T. luteum*																
Feulgen Tech.	11.2	1.5	12.7	16.1	5.8	21.9	8.7	5.7	14.4	13.3	7.0	20.3	14.4	13.1	27.5	193.6

1. *T. erectum* L., normal, Feulgen technique in present study.
2. *T. erectum* L., 3° C. for 96 hours, Feulgen technique in present study.
3. *T. erectum* L., normal, Aceto-carmine technique in study of Wilson and Boothroyd.
4. *T. erectum* L., 3° C. for 96 hours, Aceto-carmine technique in study of Wilson and Boothroyd.
5. *T. erectum* L., normal, Aceto-carmine technique in present study.
6. *T. erectum* L., 3° C. for 96 hours, Aceto-carmine technique in present study.
7. *T. luteum* (Muhl.) Harbison, normal, Aceto-carmine technique in present study.
8. *T. luteum* (Muhl.) Harbison, normal, Fuelgen technique in present study.

L.A.—Long Arm; S.A.—Short Arm; T.L.—Total Length.

Standard deviations for the total lengths of individual chromosomes in this study range from 0.5 to 1.2.

marized by Woodard (1948). The aceto-carmine technique employed by Wilson and Boothroyd (1944) in their study of differential reactivity was also used by the writer for comparative study as discussed in a later section.

OBSERVATIONS AND DISCUSSION

Normal Chromosome Complement. The morphology of the normal (non-cold treated) chromosome set of *Trillium erectum* L. (fig. 6) was carefully studied. Measurements were made of more than 100 chromosomes of each type (A, B, C, D, and E) in the 2n root tip complement. The results of these measurements are summarized in table I, 1 which shows the total length of the chromosomes as well as the length of the chromosome arms.

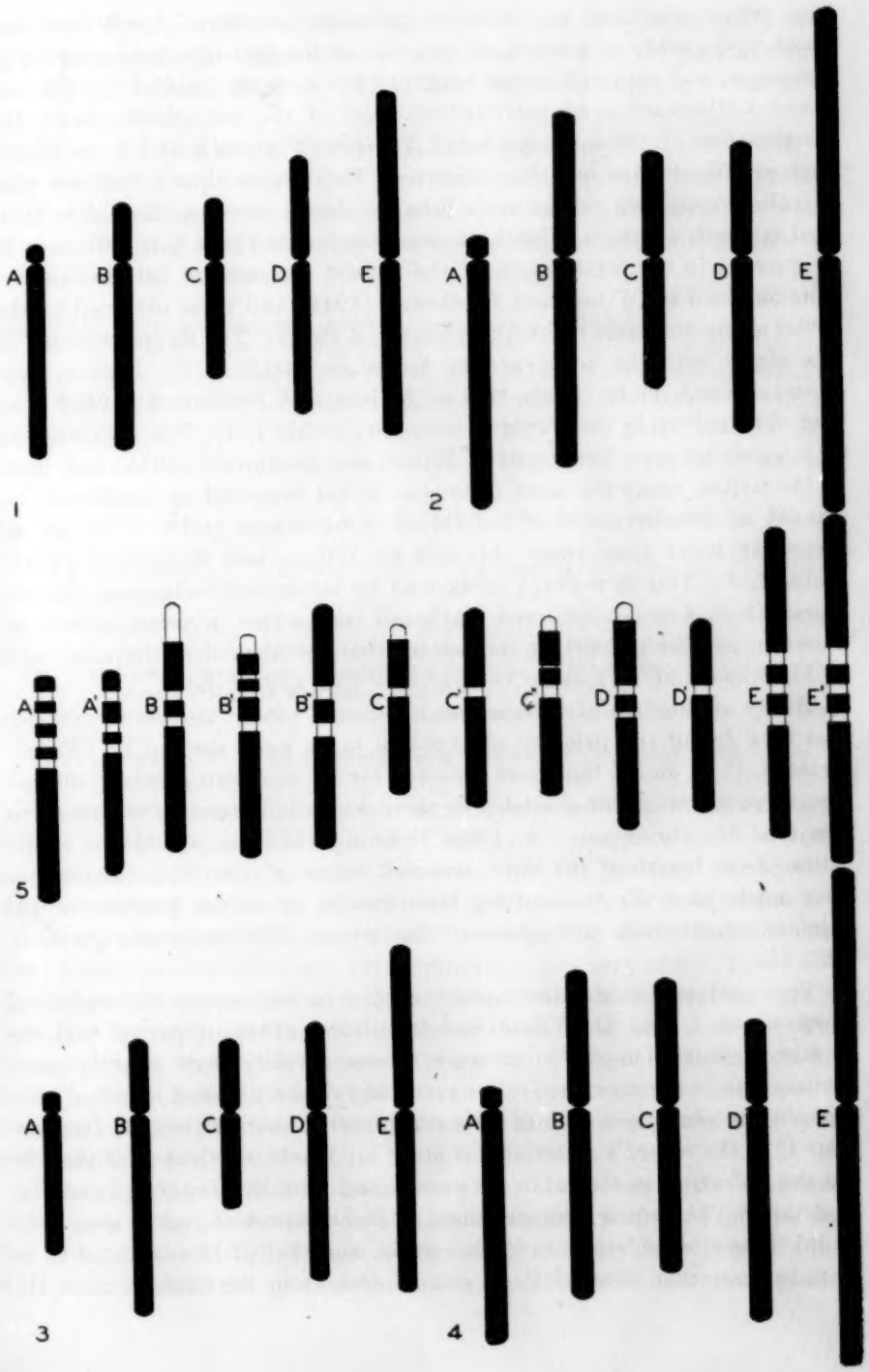
A total of 21 different plants was employed in studying the normal chromosome complement. A number of root tips were secured from each and an accurate record maintained of slides made from each plant, in order to determine whether any variations occurred. No variations of any significance were found. Included in the 21 were two plants of the albino strain which also showed no variations in chromosome size.

A diagram showing the relative lengths of the chromosome arms is given in figure 1. This reveals that the primary constriction of chromosome A is sub-terminal; those of B, C, and D are sub-median; and that of chromosome E has an almost median, actually a sub-median primary constriction.

The total length of the normal diploid chromosome set was found to be 199.4 microns (table I, 1). This figure is much lower than that found by Wilson and Boothroyd (1944) for their Canadian plants of the same species, their figure for the normal complement being 285 ± 6.9 microns (table I, 3). This difference in the total length of the normal complement, however, can be attributed entirely to the difference in the techniques employed in the two studies as will appear later. Wilson and Boothroyd (1944) used the aceto-carmine technique obtaining the results shown in table I, 3.

FIGS. 1–5. Diagrammatic analysis of chromosome morphology of *T. erectum* L. and *T. luteum* (Muhl.) Harbison based upon measurements of mitotic metaphase chromosomes. Fig. 1. Normal chromosome complement of *T. erectum* L. prepared by the Feulgen squash technique. Fig. 2. Normal chromosome set of *T. erectum* L. prepared by aceto-carmine technique. Fig. 3. Normal chromosome complement of *T. luteum* (Muhl.) Harbison prepared by the Feulgen squash technique. Fig. 4. Normal chromosome complement of *T. luteum* (Muhl.) Harbison prepared by aceto-carmine technique. Fig. 5. Chromosomes of *T. erectum L.* after 3° C. for 96 hours using the Feulgen squash technique. Types of patterns of differentially reactive segments are shown for each individual chromosome after treatment with cold. Marked contraction of these chromosomes is apparent.

All figures are drawn to scale at an approximate magnification of × 1650 after reduction.


A
B
C
D
E
1
A
B
C
D
E
2
A
A'
B
B'
B"
C
C'
C"
D
D'
E
E'
5
A
B
C
D
E
3
A
B
C
D
E
4

The writer also used the identical technique employed by Wilson and Boothroyd (1944) as a check on root tips of the same species occurring in Tennessee, and obtained a total length of 265 microns (table I, 5). Figures 1 and 2 illustrate comparatively the effect of the two techniques on the chromosomes of the same species of *Trillium*. Figures 6 and 7 are photomicrographs illustrating this difference. The figures clearly indicate that no valid comparison can be made between chromosome lengths unless identical methods of preparation have been employed. There is a difference of 20 microns in the total length of the normal complement between the results obtained by Wilson and Boothroyd (1944) and those obtained by the writer using the same technique (table I, 3 and 5). The figure obtained in this study with the aceto-carmine technique (table I, 5), however, approaches much more closely that of Wilson and Boothroyd (1944) than that obtained using the Feulgen technique (table I, 1). The difference of 20 microns between the results of Wilson and Boothroyd (1944) and those of the writer, using the same technique, is not regarded as significant, inasmuch as measurements of individual chromosomes (table I, 5) are all somewhat lower than those obtained by Wilson and Boothroyd (1944) (table I, 3). This is perhaps occasioned by measuring metaphase chromosomes which had not achieved maximum contraction, a point difficult to ascertain infallibly. Further indications that the method of preparation is highly important in making comparisons will appear later.

Study of the data of Wilson and Boothroyd (1944) reveals in addition that they found the primary constriction to be more median in Chromosomes B, C, D, and E than here reported for the southern plants. Sufficient measurements were not available in their paper to determine whether this was true for chromosome A. From their figures it is possible to obtain ratios of the length of the short arm and the long arm. Such calculations were made in order to compare their results as to the position of the primary constriction with those of the writer. The ratios are given in table II.

The most noticeable discrepancy occurs in comparing the ratios of chromosomes C and D. Wilson and Boothroyd (1944) reported that the primary constriction of chromosome C was actually very slightly more median than in chromosome D; however, the ratios are almost identical even thought the absolute length of C is considerably shorter than D. Chromosome C in the writer's material was also found to be much shorter than D, but the difference in the ratios between C and D in the Tennessee material is striking. The primary constrictions of chromosomes C and D were both found to be more sub-median in this study, and that of D was found to be more median than that of C. It can be seen from the ratios (table II)

that the differences between those based on Wilson and Boothroyd's data (1944), especially for chromosome C, and those found in the present study are entirely too great to have resulted from slight inaccuracies in measurements and calculations.

Wilson and Boothroyd (1944) found the two arms of chromosome E to be so nearly the same length that they disregarded the difference. Actually a noticeable difference is present in the writer's preparations: the ratio between the long arm and short arm is 95:100, the actual difference in length being 0.7 micron.

TABLE II. *Short-arm, long-arm, ratios in chromosomes of Trillium erectum L. before and after cold treatment.*

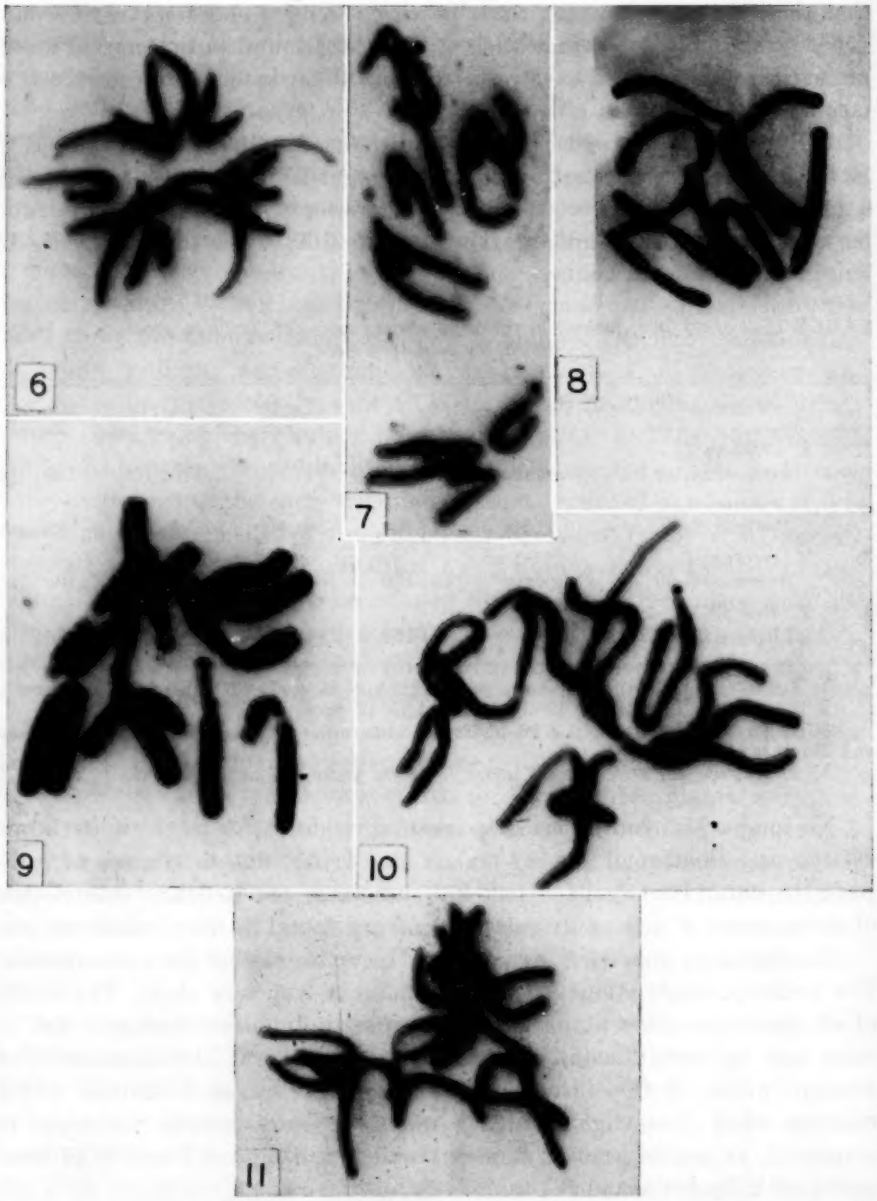
	Material	Chr. A	Chr. B.	Chr. C	Chr. D	Chr. E
1.	*T. erectum* L. Aceto-carmine	no data	40:100	77:100	76:100	100:100
2.	*T. erectum* L. Feulgen Tech.	10.6:100	31:100	54:100	67.5:100	95:100
3.	*T. erectum* L. Aceto-carmine	no data	45:100	100:100	64:100	100:100
4.	*T. erectum* L. Feulgen Tech.	7:100	52:100	61:100	63:100	90:100

1. *T. erectum* L., normal, aceto-carmine technique in study of Wilson and Boothroyd.
2. *T. erectum* L., normal, Feulgen technique in present study.
3. *T. erectum* L., 3° C. for 96 hours, aceto-carmine technique in study of Wilson and Boothroyd.
4. *T. erectum* L., 3° C. for 96 hours, Feulgen technique in present study.

No comparison can be made between chromosome A in the material of Wilson and Boothroyd (1944) and of the writer, due to absence of comparative data. It may be noted, however, that the primary constriction of chromosome A is the only sub-terminal one found in the chromosome set.

No secondary constrictions normally occur on any of the chromosomes. The primary constrictions are very prominent, yet very short. The width of all the chomosomes prepared by the same technique is constant, that is, there are no variations in width among the several chromosomes. The average width of the chromosomes using the Feulgen technique is 1.4 microns while it is slightly higher when the aceto-carmine technique is employed, as can be seen in figures 1 and 2 and figures 7 and 9 as compared with figures 6 and 8.

The morphological differences between the chromosome sets summarized in the preceding paragraphs, in the Canadian and Tennessee plants, led the writer to think that the two studies might possibly have been dealing with entirely different plants. Herbarium specimens of Canadian plants



FIGS. 6–11. Photomicrographs of chromosome complements of *T. erectum* L. and *T. luteum* (Muhl.) Harbison. Fig. 6. *T. erectum* L. normal after using the Feulgen technique. Fig. 7. *T. erectum* L. normal after using aceto-carmine technique. Fig. 8. *T. erectum* L. after 3° C. for 96 hours using the Feulgen technique. Fig. 9. *T. erectum* L. after 3° C. for 96 hours using aceto-carmine technique. Fig. 10. *T. luteum* (Muhl.) Harbison normal after using aceto-carmine technique. Fig. 11. *T. luteum* (Muhl.) Harbison normal after using the Feulgen technique.

furnished by Dr. Pierre Dansereau along with plants used in this study were sent to Dr. Wm. A. Anderson of Iowa State University and to Dr. S. J. Smith of Syracuse University for identification. Both identified all plants as *T. erectum* L.

Differential Pattern. The position of the differential segments of the chromosomes resulting from cold treatment appeared to be almost constant within the group of plants studied. Figure 5 represents diagrammatically the variation in chromosome complement of *T. erectum* L. after exposure to 3° C. for 96 hours; the position and average size of the differential segments are represented in the diagrams which are drawn to scale. Where more than one chromosome is illustrated for each type, more than one differential pattern appeared in that particular chromosome after treatment.

It is apparent in figure 5 that the differential pattern varies somewhat, and that in chromosomes C and D instances were found where no differential segments appeared after cold treatment. In the case of chromosome C the number of chromosomes in which no differentiation appeared amounted to 10.9% while in chromosome D the number amounted to 28.7%. These percentages are based upon study of more than 100 chromosomes of each type. This apparently indicates that chromosomes A, B, and E are more readily affected by cold treatment than are chromosomes C and D.

It can be seen from the diagrams that not all cold-treated nuclei contain the same number of visibly differentiated segments. The total maximum number of such regions in the diploid nucleus was found to be 24 while in 83.2% of the total number of chromosomes measured only 20 such segments appeared regularly. These results differ markedly from those of Wilson and Boothroyd (1944). They found a total number of 42 differential segments in the diploid nucleus with 24 of the total appearing regularly. Furthermore, in this connection, if each chromosome is conconsidered individually, and if comparisons are made between the Canadian and Tennessee plants, differences are apparent for all plants. Chromosomes A, however, probably shows fewer discrepancies than any of the others. As shown in the diagram three secondary constrictions or differentially reactive segments appeared regularly (fig. 5, A), and in only six chromosomes out of a total of 116 were two secondary constrictions found. Wilson and Boothroyd (1944) also found three secondary constrictions in the same position. They found instances, however, where the differential segments fused making one long differential segment. No examples of this type were observed in the present study. In neither case were differentiated segments found to be distal to the primary constriction.

In chromosome B Wilson and Boothroyd (1944) regularly found one terminal and three interstitial segments. The writer, however, found the terminal and one interstitial constriction to be of regular occurrence (fig. 5, B). In 12 chromosomes out of a total of 100, however, two interstitial segments appeared (fig. 5, B′), one interstitial on either side of the primary constriction. In 11 out of the 100 chromosomes the terminal constriction failed to appear, but the interstitial one in the long arm remained (fig. 5, B″). Wilson and Boothroyd (1944) also found two segments which were not regular in their appearance: one of these occupied the distance between the terminal constriction and an interstitial one. Therefore, when this particular sporadic differential segment appears, the terminal and the closest interstitial one fuse, thus forming one long terminal segment. This might possibly explain the condition in the 12 chromosomes represented by the type B′ illustrated in figure 5. Measurements of the relative lengths seem to indicate that this is true. In the regularly recurring pattern, however, Wilson and Boothroyd (1944) found two differential segments more than were observed in the writer's material.

Chromosome C (fig. 5) presents a simpler pattern. Ninety-six chromosomes out of a total of 110 showed only a terminal differential segment (fig. 5, C). Twelve out of the 110 were not affected at all (fig. 5, C′), and two out of the total showed the terminal constriction plus a very short interstitial segment (fig. 5, C″). The latter, one terminal and one interstitial segment, is the pattern found regularly by Wilson and Boothroyd (1944) in chromosome C in their material.

In chromosome D (fig. 5, D) one terminal constriction was found in the short arm and one interstitial or sub-median segment appeared on the the long arm in the writer's preparations. These were the only two differtial segments to appear in this chromosome, and both were differentiated regularly. As has already been pointed out, 29 chromosomes out of a total of 109 were not affected by the cold treatment (fig. 5, D′). Wilson and Boothroyd (1944) observed a sub-median constriction and a sub-terminal one on the long arm of chromosome D in addition to the two observed by the writer, thus making a total of four recurring regularly in their plants. They also found another terminal segment which was irregular in its appearance which, when present, was fused with the sub-terminal one.

The differential segments in chromosome E (fig. 5, E) appeared equidistant from the primary constriction. Two sub-median segments occurred, one being in each chromosome arm (fig. 5, E). This was true in 100 chromosomes out of a total of 109. In addition to these two, a smaller sub-median segment appeared in the long arm in nine of the 109 chromosomes (fig. 5, E′). The latter was more terminal than the sub-median segment which ap-

peared regularly. Wilson and Boothroyd (1944) found three corresponding segments in their studies of chromosome E as well as an additional one which was of regular occurrence. The last is similar to the one described by the writer as appearing irregularly (fig. 5, E′), except that it is found on the opposite arm. Both Canadian and Tennessee material thus exhibit one regularly appearing constriction in each arm of chromosome E. Wilson and Boothroyd (1944) also found a terminal and an additional interstitial segment appearing irregularly.

Inasmuch as the two arms of chromosome E are so nearly the same length it is possible to mistake the arm in which the third interstitial segment appears; the irregular appearing constriction might have appeared in either chromosome arm. If this were true, the exception in the present study would correspond to what Wilson and Boothroyd (1944) regard to be the rule.

Homologous chromosomes always presented the same differential pattern regardless of whether it was the regularly or irregularly appearing one. This is significant in that it indicates the pattern is basic and inherent for the chromosomes. However, the fact that the irregularly appearing pattern also is found in both homologous chromosomes is difficult to explain.

In summarizing the comparison between the two studies it is obvious that the behavior of chromosome A upon cold treatment was the same in both Wilson and Boothroyd's (1944) and the writer's observations. What Wilson and Boothroyd's (1944) found to be the rule in chromosomes B, C, and E, this study revealed it be the exception, and in chromosome D no similar patterns were found.

Contraction. The study of differentiation was restricted to the mitotic metaphase chromosomes. Measurements of the chromosome complement were made after treatment at 3° C. for 96 hours. Table I shows, in addition to the normal chromosome data referred to in the preceding paragraphs, the length of the individual chromosomes after cold treatment, the total length of the chromosome set, and the length of the long and short arms.

A comparison of the figures in table I reveals the degree of contraction resulting from cold treatment. The total average length of the diploid chromosome set before cold treatment was 199.4 microns (table I, 1) while after 3° C. for 96 hours the total average length was 186.4 microns in Feulgen preparations (table I, 2). Expressed as percentage of contraction this would mean that the chromosomes measured 93.5% of their total length after treatment. Wilson and Boothroyd (1944) found a greater degree of contraction resulting from cold treatment; their measurements (table I, 3)

show the total length to be 285 ± 6.9 microns before treatment and 234 ± 4.5 microns or 82.1% afterwards (table I, 4).

The difference between the results of Wilson and Boothroyd (1944) and those of the author after cold treatment are again the results of using different techniques as clearly indicated in table I, 2, 4, 6. In an attempt to explain this discrepancy the writer employed the aceto-carmine along with the Feulgen technique to obtain comparative data. The total length of the chromosome complement using the aceto-carmine technique on the root tips of the Tennessee plants of *T. erectum* L. is close to that listed for Wilson and Boothroyd (1944) (table I, 4, 6). The total length was 201.2 microns on *T. erectum* L. used in this study and 234 ± 4.5 microns on the material of Wilson and Boothroyd (1944). In the writer's opinion this is not a very significant difference inasmuch as all measurements are slightly lower than those of Wilson and Boothroyd (1944).

Furthermore, it is again possible to compute ratios between the long and short arms of the chromosomes after cold treatment from the figures given by Wilson and Boothroyd (1944) and from the writer's data (table II). If these ratios are compared it will be found that very little variation exists between the two, that is, the ratios increased or decreased in about the same proportions in the two sets of figures (normal and cold treated).

It should be noted in passing that the ratios for chromosomes A, D, and E decrease slightly while for chromosomes B and C the ratios remain about the same after cold treatment.

The increase and decrease in the ratios seem to indicate that the differential segments undergo less contraction during cold treatment than do the non-affected portions of the chromosomes. Chromosome A which shows the greatest decrease in its ratio has in the long arm three regularly occurring differential segments, while none are present in the short arm. Chromosome C shows an increase in its ratio which may be accounted for by the fact that only one differential segment appears, namely that in the short arm. One differential segment appears in both the short and long arm of chromosome B, the one in the short arm being almost twice the length of the one in the long arm. This fact would account for the increase in the ratio just as in chromosome C. The differential segments are approximately the same length in the two arms of chromosome E, and, as expected, the ratio remains approximately the same.

Wilson and Boothroyd (1944) compared the length of chromosome arms which had differential segments with those having none to show that contraction produced by cold is not uniform throughout the chromosome complement. The results in the present study were similar. As was shown

in the preceding paragraph, the ratio of the length of the short arm to the long arm in chromosome C is 54:100 in untreated material and 61:100 in treated material. The corresponding ratios of B short to C long arm are 50:100 and 68:100 respectively.

It is significant that chromosome D shows the greatest degree of contraction of any of the chromosomes. The difference in the total length between the normal and treated chromosome is 5.4 microns. This can be accounted for, however, by the fact that 28.7% of the chromosomes do not show any differentially reactive segments. This means, as has been pointed out in the preceding paragraphs, that those chromosomes which did not show any differential segments underwent a greater degree of contraction. Actually their length after treatment was only 83.8% of the length before treatment.

A fact that has not been pointed out previously is that the primary constriction is actually a region which is differentially reactive. As shown in figures 1, 2, 3 and 4 the primary constrictions of untreated chromosomes appear to be very short. Figure 5 reveals them to be much longer after cold treatment. The length of the primary constriction is about the same as the regularly appearing differential segments in treated chromosomes. The diagrams of Wilson and Boothroyd (1944) do not show this to be true of their material. Actually this would mean that 10 more differential segments should be added to the number which appear regularly after treatment in the writer's material. This would make a total of 30 such segments.

The diagrams (fig. 5) depicting the range of differential patterns indicate that the length of the differential segments varies from 0.42 to 0.83 microns, the greater percentage of them being 0.83 microns.

Figure 5 indicates clearly the degree of variation in the differential segments. An accurate record was kept of every chromosome measured and the plant and root tip from which it came. Reference to these records reveals that not all chromosomes having a given differential pattern occur within the same plant or within the same root tip; any combination of differentially reactive segments shown in the diagrams illustrating the various patterns may occur.

Chromosome fragmentation was observed in this study in root tip mitoses of two different plants. The fragenmtation, however, cannot be attributed to the cold treatment because the root tips of one plant were untreated, while those of the other had been exposed to cold. The chromosomes from root tips which had received no cold treatment were perfectly normal as to length, width, positon of the primary constriction, etc. In no instance where chromosome fragments were present did chromosome D show any

intercalary segments. The two fragments when present were usually located on or very near chromosome D which may or may not have any significance.

No correlation was found between the number of visibly differentiated segments and the number of chromocenters in the resting nucleus with which Darlington and LaCour (1940) associated them. The maximum number of chromocenters counted was approximately 14 or 15 while the number of differential segments ranges from 20 to 24.

Trillium luteum (Muhl.) Harbison. The morphology of the normal chromosome complement of *T. luteum* (Muhl.) Harbison was studied using both the Feulgen and the aceto-carmine techinques. This study was made in order to determine whether the difference occasioned by the two different techniques in *T. erectum* L. would occur in another species of *Trillium*. The results of this phase of the study are also included in table I, 7 and 8. The total length of the chromosome complement is 193.6 microns in Feulgen preparations (fig. 3) while by the aceto-carmine technique the total length is 273.4 microns (fig. 4). If this result is expressed as a percentage, the total length with the Feulgen technique will be 71% of that obtained by the aceto-carmine technique. These results approach very closely those found with *T. erectum* L., the difference between the two techniques on *T. erectum* L. being 30%. This indicates that the difference between the two techniques may be constant. A pictorial comparison of the results of the two techniques may be observed in the photomicrographs (figs. 6–11); however, the chromosomes of figure 10 have undergone some stretching as a result of the squash technique. Certain chromosomes can be singled out which have apparently undergone no stretching and comparison may be made with these.

Another significant feature of this phase of the study is the similarity between the morphology of chromosomes of *T. erectum* L. and *T. luteum* (Muhl.) Harbison. The total length of the individual chromosones of *T. erectum* L. by the Feulgen technique is 199.4 microns while the total length of those of *T. luteum* (Muhl.) Harbison using the same technique is 193.6 microns. These measurements are entirely too close to separate these species on the basis of total length of the chromosome set. There are differences between the long- short-arm ratios and in the total length of the individual chromosomes between the two species. Chromosomes A and B (figs. 1 and 3) show the greatest variations. The writer, however, is in agreement with Barksdale (1938) when he states that the view that minor floral and vegetative variations peculiar to any one species should be reflected in the morphology of one or several of the chromosomes is a rather naive one. Before the assumption can be made that different species of the genus *Trillium* can be separated on the basis of chromosome morphology, a very thorough cytological investigation must be made of every species within the genus.

SUMMARY

1. Morphological differences exist in the normal chromosome complement of *T. erectum* L. growing in Tennessee and *T. erectum* L. growing in Canada. Taxonomically the plants are identical insofar as the conventionally employed morphological characters are concerned.

2. In obtaining valid comparative data as to chromosome morphology identical techniques must be employed. The Feulgen and the aceto-carmine techniques give results which differ by approximately 30% in the *Trillium* species studied. This is shown in both the study of *T. erectum* L. and *T. luteum* (Muhl.) Harbison. There is no difference with these techniques, however, as to the position of the primary constriction; the ratio between the long arm and short arm remains the same.

3. The pattern of differential segments produced by cold treatment cannot be employed as a valid or even useful taxonomic indicator for distinguishing species, for too many differences exist in the regularly recurring pattern in the Canadian *T. erectum* L. and that in plants of the same species growing in Tennessee.

4. The primary constriction also behaves like a region of differential reactivity upon exposure to cold.

5. The differential segments themselves undergo less contraction than the non-affected portions of the chromosomes upon exposure to cold.

6. The morphology of the normal chromosomes set of *T. erectum* L. differs slightly from that of *T. luteum* (Muhl.) Harbison; however, the total length of the two complements is the same.

ACKNOWLEDGMENT

The writer wishes to take this opportunity to express his appreciation to the late Dr. Thomas M. Woodard, Jr., who suggested this study and under whose direction most of it was carried on. He also wishes to express his gratitude to Dr. Harold C. Bold for suggestions and criticisms in the completion of the problem and in preparation of the manuscript. Thanks are also due to Dr. Frederick T. Wolf for reading and criticizing the manuscript.

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RANGE EXTENSIONS OF CAREX NEUROCHLAENA HOLM

MAXIMILIAN G. DUMAN

Carex neurochlaena was described by Holm (1904) from specimens collected by Macoun above Rink Rapids on the Yukon River, Yukon. After its description it was unreported for nearly forty years until collections from both eastern and western Canada were reported nearly simultaneously. Eighteen collection numbers made by Dutilly, O'Neill, and the author in eastern Canada at Wakeham Bay, Churchill, Chesterfield, Baker Lake, and Repulse Bay were reported by Duman (1941). Hultén (1942) refers to the collections of A. E. Porsild, and gives its range "from Yukon to the N. W. Territories." He does not include it in the flora of Alaska. Porsild (1943) cites seven collection numbers, and gives its range in the Northwest Territories "from the Mackenzie River Delta east to Anderson River, south to Great Bear Lake."

A short discussion of the status and distribution of *Carex neurochlaena* appeared in this BULLETIN two years ago (Duman 1947). Since that time the identification of several noteworthy collections made by Arthème Dutilly, Hugh O'Neill, and Ernest Lepage has extended its range south into the James Bay region, north into Baffin Island, and west into Alaska.

In 1942 Dutilly collected a single specimen of *Carex neurochlaena* at Lake Harbor, Baffin Island (*Dutilly 9125a*). This is a new addition to the flora of Baffin Island.

During the summer of 1946 Dutilly and Lepage collected *Carex neurochlaena* on the west coast of James Bay at Lake River (*Dutilly & Lepage 16579, 16672*), and at Fort Albany (*Dutilly & Lepage 16011*). This is a southern extension of range for this northern species.

In 1947 Dutilly, O'Neill and Lepage collected *Carex neurochlaena* at Nebesna Road, Mile Post 91, Alaska (*Dutilly, O'Neill & Lepage 21605*). This location is just across the Alaska-Canadian border from the type locality in the Yukon. In 1948 Lepage collected this species at Umiat, Colville River (69° N. Lat.), Alaska (*Lepage 23775*). These are the first reported collections from Alaska, and hence represent a new addition to the flora of Alaska.

Lepage (personal communication) confirms our observation that solitary culms growing in wet sphagnum are characteristic of this inland species, and suggests that this may be one of the reasons that it has been frequently overlooked.

In some of the collections made before this species was recognized in the field the material is rather scarce, as would be expected in a species

with scattered culms. In other localities, however, it is far from being rare, as for example the abundant material in the ten collection numbers made by Dutilly and the author at Churchill. Lepage informs us that it is commonly scattered through the sphagnum bogs at Umiat, Alaska.

Although this species is now known over a wide range, the collection localities are widely separated. Undoubtedly a careful search in wet sphagnum bogs for its solitary, scabrous culms, bearing green to brown perigynia which are gradually smooth-beaked, the beak having a very characteristic slight bend, will uncover new stations, and give us a more true picture of the actual distribution of this interesting species.

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CRITICAL NOTES ON SOME PLANT RUSTS

M. J. THIRUMALACHAR

1. On Scopellopsis Dalbergiae Ramk. & Ramk. and Mainsia Pterocarpi Thirum. The genus *Scopellopsis* was established by Ramakrishnan and Ramakrishnan (1947a) for a rust on *Dalbergia paniculata* Roxb. Subepidermal uredia and intraepidermal telia with one-celled, stipitate, colourless spores borne on basal cells were given as important characters. Thirumalachar (1947) described the rust *Mainsia Pterocarpi* earlier from Mysore, South India. A careful restudy of *Scopellopsis Dalbergiae* and *Mainsia Pterocarpi* indicated that the two rusts were identical and the hosts probably closely related. In a recent paper Thirumalachar and Cummins (1949) discussed the taxonomic significance of sporogenous basal cells in the Uredinales and concluded that the clustered condition only represented one of the modes of spore development, without having generic significance. Evidence was presented for not maintaining the genus *Scopellopsis*.

Thirumalachar (1947) described the same rust as *Mainsia Pterocarpi* because of the intraepidermal telia and the hyaline, stipitate teliospores. The genus *Mainsia* Jackson, however, includes both forms with intraepidermal and with superstomal sori, the latter resembling *Gerwasia* Raeb. Further studies are needed to elucidate and stabilize its generic characters. Though pycnial stages are known for *Scopellopsis Dalbergiae*, its resemblance to *Maravalia achroa* (Syd.) Arth. & Cumm. is close. In the collections of *Maravalia achroa* made by Clemens in the Philippines there are distinct sporogenous basal cells in the telia. The only differentiating features in *Maravalia achroa* are the lack of paraphyses and the subepidermal position of the telia. Pycnial stages will be necessary to confirm whether the rust is a species of *Maravalia* or of *Scopella*. For the present, to indicate the close relationship between the two rusts, the species on *Dalbergia paniculata* is placed under *Maravalia:* **Maravalia Pterocarpi** (Thirum.) Thirum. comb. nov. (*Mainsia Pterocarpi* Thirum., *Scopellopsis Dalbergiae* Ramk. & Ramk.)

2. On Maravalia ascotela (Syd.) Mains. In a recent study, Ramakrishnan & Ramakrishnan (1947b) have discussed the need for a change of nomenclature of *Maravalia ascotela* (Syd.) Mains (Mains 1939) which had been transferred to *Chrysocelis ascotela* by Thirumalachar (1942a), on the basis of a cytological study. Ramakrishnan & Ramakrishnan noted the basal cells and transferred the rust to *Scopella* as *S. ascotela* (Syd.) Ramk. & Ramk. Since the rust has subepidermal pycnia, in contrast to the subcuticular ones found in the type of the genus, they emended the generic de-

scription of *Scopella* Mains to include both subepidermal and subcuticular pycnia, citing as supporting evidence the example of *Ravenelia* which has been referred to (Thirumalachar & Cummins 1949). The emendation of the genus is undesirable since it is the pycnial character that is of primary importance and the presence of basal cells is secondary only. Since the elongation of the basal cells into pedicel-like structures can be traced only in well-stained microtome preparations, it seems advisable for taxonomic purposes to follow Mains' (1939) treatment.

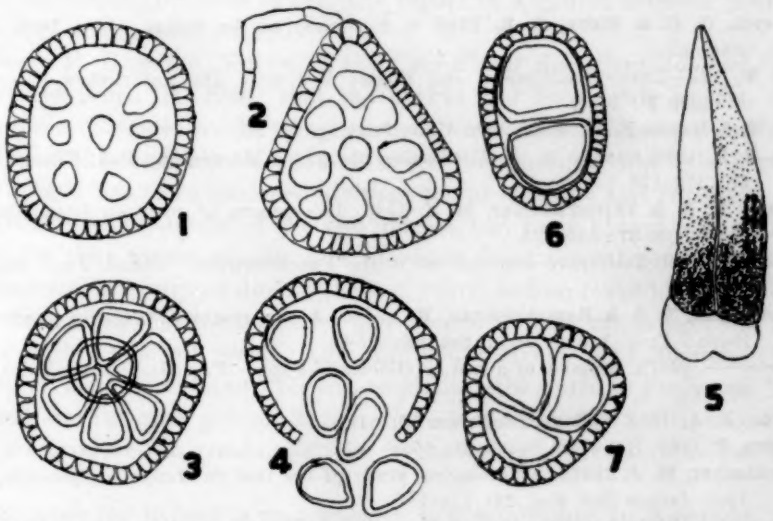
3. On Mehtamyces Mundkur & Thirum. The genus *Mehtamyces* was established for a rust on *Stereospermum suaveolens* Wall. in India by Mundkur & Thirumalachar (1945). The genus is characterized by the presence of aparaphysate uredia with urediospores borne in clusters on sporogenous basal cells, and non-erumpent, subepidermal telia developing as large indefinite crusts. The teliospores are produced in chains of 4–8 spores, yellowish-brown in color and compactly grouped. Since the sporogenous basal cells, either within the uredia or telia, have been shown to be without generic significance, the rust was restudied.

The telia provide the chief differentiating character. The telial crusts externally resemble the type found in many species of *Pucciniastrum*, such as *P. Coriariae* Diet. and *P. Castaneae* Diet. in forming large indefinite patches. Some of the telia on *Stereospermum* leaves measure up to 3 cm. Telia of this type are quite distinct from the lenticular crusts found in the genera *Phakopsora* Diet., *Angiopsora* Mains, and *Bubakia* Arth. Even the initial stages of telial development somewhat resemble that of *Pucciniastrum* species, as described by Pady (1933). The telial initials are formed between the epidermis and palisade layers. In *Pucciniastrum*, a series of vertical septations takes place resulting in a flattened telial crust, while, in *Mehtamyces*, these produce vertical chains of spores in basipetal succession. Further, in *Mehtamyces*, the teliospores are resting spores, and the uredia are without the characteristic peridium of *Pucciniastrum*. Therefore, even if the sporogenous basal cells of the uredia are disregarded, the telial characters separate the genus *Mehtamyces* from other genera.

4. Puccinia on Chomelia asiatica O.Kze. A rust on *Chomelia asiatica* was described by Thirumalachar (1942b) as a new species under the name *Puccinia Chomeliae*. A comparative study of *Puccinia spongiosa* Berk. & Br., deposited in the Arthur Herbarium and in the Mycological Collections of the U.S.D.A., indicates that the two resemble each other closely. Slight variations in the sizes of the teliospores have been noticed in some of the collections but considering the general range of variability, it is desirable to merge *P. Chomeliae* Thirum. with *P. spongiosa*.

5. On Uleiella Schroet. The genus *Uleiella* was founded by Schroeter (1894) for a fungus parasitic on shoots of *Araucaria imbricata* in Brazil,

collected by Ule. The fungus forms sooty black spore mass within the host tissue. The spores are subglobose to spherical, chestnut-brown, and inclosing 6–8 sporidia (?). *Uleiella paradoxa* Schroet. was designated as the type, and the fungus was placed under the Uredinales. Saccardo (1897) in listing the genus, doubtfully assigned it under the smuts. Another species, *Uleiella chilensis* Diet. & Neger (1899), was established for a similar fungus on *Araucaria imbricata* in Chile. Dietel (1897–1900), in his treatment of the "Hemibasidii", briefly described the development of the spores within the host at the ends of hyphae. Though the spores have not been germinated, Dietel considered the genus as a doubtful member of the Hemibasidii along with *Meria* Vuillem., which was once placed under that order. However, recent studies have shown that *Meria* is a moniliaceous fungus.



FIGS. 1–4. Developmental stages of the spores of *Uleiella paradoxa*. × 300. FIG. 5. Sporophyll of *Araucaria imbricata* showing infection. × 1. FIGS. 6, 7. Spores of *Uleiella chilensis*. × 300.

Authentic specimens of *Uleiella paradoxa* and *U. chilensis* (Rabenhorst-Winter-Pazschke, *Fungi Europei 3940* and Rabenhorst-Pazschke, *Fungi Europei et Extraeuropei 4303*) deposited in the Mycological Collections of the U.S.D.A. were studied. Sections through the infected sporophylls (fig. 5) of *U. paradoxa* revealed that the spores develop from the hyphae bordering the lacunae formed within the host tissue. The spores are spherical to subglobose, yellowish to chestnut-brown, and with a deeply pitted spore wall which imports a tuberculate appearance. As the spores mature, 6–14 small endospores appear within the spore cavity. These are at first scattered (figs. 1, 2) but as they enlarge in size, they occupy the entire space (figs.

3, 6, 7). The endospores are somewhat angular due to mutual compression. In later stages, the outer sporecoat bursts and releases the endospores (fig. 4). The mode of development of the endospores resembles the free cell formation within an ascus, though it is not possible to get all the details from herbarium material.

The genus *Uleiella* has been doubtfully placed under either rusts or smuts by Schroeter, Dietel, Saccardo, Ainsworth & Bisby (1945), and others. The morphology of the spores indicates that it does not belong to either of them.

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HYBRID OF KALANCHOË DAIGREMONTIANA AND K. VERTICILLATA

J. T. BALDWIN, JR.

A photograph of two *Kalanchoë* species and their hybrid appeared in the *Cactus and Succulent Journal* for August, 1939 (**11**: 64). Though the plants were young, the parents were obviously referable to *K. Daigremontiana* Hamet & Perrier and *K. verticillata* Scott-Elliot, and the hybrid seemed intermediate in leaf characters. It was known that *K. Daigremontiana* is a diploid biennial or triennial and that *K. verticillata* is a tetraploid perennial (Baldwin 1938). The report of a hybrid between them was therefore of peculiar interest.

Scott E. Haselton, Editor of the *Cactus and Succulent Journal*, wrote (letter of April 24, 1940) that the hybrid had been made by Dr. A. D. Houghton (then deceased), whose gardens were in San Fernando, California, and from those gardens Mr. Haselton sent me parental and hybrid plants. The hybrid was more intermediate than the photograph had revealed.

Detailed comparison of the two species and their hybrid was planned. And for that reason plants were obtained from several sources. But the project was interrupted during the war years, and on resumption of work it was discovered that the gardener had discarded from the greenhouse all of these highly efficient weeds. And who could blame him? Swingle (1934) called *H. Daigremontiana* "the easiest plant in the world to propagate." The hybrid and its other parent, however, are just as readily multiplied. Plantlets are produced in great quantities on the leaves of all the individuals concerned.

Because the hybrid is undoubtedly well established in American horticulture (it was, for example, found in a Roanoke, Virginia, greenhouse), and because the hybrid and its parents are excellent experimental material, a drawing of the hybrid made by Eduardo Salgado is published here (fig. 1).

Baldwin (1938) reported *K. Daigremontiana* to have $2n = 34$, $n = 17$ and *K. verticillata* to have $2n = 68$. Uhl (1948) recorded $n = 17$ in *K. Daigremontiana*. This species as sent me by Mr. Haselton had $2n = 34$ (fig. 2); *K. verticillata*, $2n = 68$ (fig. 4); the hybrid, $2n = 51$ (fig. 3). As expected, the hybrid was triploid and thus intermediate between its parents. The hybrid from Roanoke, Virginia, was likewise triploid. *K. Daigremontiana* from other sources in California and Texas was diploid, and *K. verticillata* from other sources in California and from Michigan State College was tetraploid. The chromosome numbers determined for these two species are apparently constant. But all the representatives of each species in the United States are

FIG. 1. *Kalanchoe Daigremontiana* × *K. verticillata*, drawn natural size by Eduardo Salgado and reduced to × 0.5 in reproduction.

FIGS. 2–4. Chromosomes of parents and hybrid in Kalanchoë. FIG. 2. $2n = 34$ in *K. Daigremontiana*. FIG. 3. $2n = 51$ in the hybrid. FIG. 4. $2n = 68$ in *K. verticillata*. × 4900.

likely to be the products in each case of single-plant introductions into the country. If in nature *Kalanchoë* follows the pattern determined for most of the Crassulaceae that have been subjected to extensive cytogeographic analysis, it would not be surprising to find more than one intraspecific chromosomal race in any given species.

Kalanchoë, with perhaps more than a hundred valid species, is fairly popular in the United States. "The species exhibit a wide range of characters, though the plants are much alike in their chromosomal make-up. *Kalanchoë* appears, therefore, to be an excellent group to hybridize interspecifically. The flowers would offer no technical difficulty in breeding experiments. Valuable hybrids could be preserved by vegetative means. The genus, no doubt, has a future of real horticultural interest" (Baldwin 1938).

SUMMARY

Dr. A. D. Houghton made a hybrid some years ago in California of *Kalanchoë Daigremontiana* ($n = 17$, $2n = 34$) and of *K. verticillata* ($2n = 68$) that is triploid ($2n = 51$) and has intermediate characters. That hybrid is in the American horticultural trade.

Kalanchoë is a promising genus for interspecific hybridizing.

COLLEGE OF WILLIAM AND MARY
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CYTOGEOGRAPHY OF EMILIA IN WEST AFRICA

J. T. BALDWIN, JR. AND BERNICE M. SPEESE

Garabedian (1924), in the most recent revision of *Emilia* Cass., recognized twenty-three species and regarded *Emilia* "more as an association of allied species than as a distinct genus." It has close affinities with *Gynura* and *Senecio* and is difficult to interpret from herbarium material alone. As seed become available we plan to grow the various representatives of this genus and to investigate their chromosomes.

Afzelius (1924) reported *n*-numbers of 5 chromosomes for *E. sagittata* (Vahl) D. C. and for *E. sonchifolia* (L). DC. Baldwin (1946) recorded that $2n = 10$, $n = 5$, for *E. sonchifolia*, and $2n = 20$ for *E. coccinea* (Sims) Sweet and discussed the cytogeographic occurrence of these two species in the Americas.

During 1947–1948, as Horticulturist, Economic Mission to Liberia, U. S. Department of State, the senior author travelled extensively in West Africa and, incidental to his assignment there, observed *Emilia* and made a few collections. Plants for cytological study have been grown in our greenhouse at the College of William and Mary. Specimens will be deposited in the herbaria of several institutions: Royal Botanic Gardens at Kew, Jardin Botanique de l'État at Brussels, U. S. National Arboretum, Smithsonian Institution.

Hutchinson and Dalziel (1931) listed three species of *Emilia* for tropical West Africa: *E. sagittata*, *E. sonchifolia*, and *E. guineensis* Hutch. & J. M. Dalziel. Baldwin examined at Kew the type of the last-named species (*Caille 14702*, Bowal to Bouria, French Guinea, Nov. 1905) and judged the specimen not referable to *Emilia*. In the opinion of Dr. R. Fosberg the plumose pappus and imbricate involucre of *Caille 14702* prevent inclusion of the specimen under *Emilia* (conversation). Hutchinson and Dalziel (1931) cited six collections for *E. guineensis*, all from French Guinea, and made *Lactuca tenerrima* A. Chev. synonymous with it; no further mention will be made by us of this entity. *Emilia* sp. is included here as an addition to the West African flora.

Of the three representatives of *Emilia* accepted for West Africa only *E. sagittata* seems not to be a weed. This species is widely distributed as an integral part of the flora. Along the trails in Liberia or beside the roads in French Guinea and along those leading inland from the coast of Nigeria, the cadmium yellow heads of *E. sagittata* frequently attract attention. But during the dry season—December to March in Liberia—this species is rarely in flower. Usually small populations of this plant occur, but some-

times a single individual is present. And in August 1947, a few miles east of Tappita, in the Eastern Province of Liberia, Baldwin saw thousands of flowering plants of this species growing among marsh vegetation. The plant itself, aside from its striking flowers, is not attractive: it stands laxly erect and when among other herbs may rise to several feet. The following collections were made:

Baldwin 5933 Liberia: Montserrado Co.: between Monrovia and Harbel, June 6, 1947. *7099* Liberia: Eastern Province: Tchien District: Monrovia-town, August 10, 1947. *9747* French Guinea: midway between N'Zérékoré and Macenta, October 13, 1947. *12012* Nigeria: Abeokuta, April 28, 1948.

Seedlings from *Baldwin 5933* were grown, and their chromosomes investigated by Speese: $2n = 10$, $n = 5$ (figs. 1–3). These results agree with previous reports.

E. sonchifolia is a widespread weed in tropical areas and is generally considered to be of Old World origin. However, in most of West Africa it is not common. Although Baldwin walked throughout Liberia (with an area of about 37,000 square miles), he found only three small populations of this species. There the plant seems restricted to sandy soils largely free of other plants and in the vicinity of coastal towns. In the Americas *E. sonchifolia* is often in comparable situations, but it is sometimes far inland, as in the Amazon Valley (Baldwin 1946). And at some places it competes rather well with other species: it was, for example, observed in 1947 among rank vegetation beside the airfield at São Luis de Maranhão in Brazil.

At first thought the extremely limited distribution of *E. sonchifolia* in Liberia is surprising, for over the centuries the natives have engaged in a "shifting agriculture" whereby ecological situations seemingly favorable for this weed have been created in abundance. But unless the human population is dense enough to carry on intensive cultivation, "bush rotation" would not be conducive to establishment of this weed. Fortunately for conservation reasons this has not been true: the native population is estimated to be under a million individuals. Moreover, it has been discovered (Baldwin 1946) that *E. sonchifolia* tends to spread along routes of considerable travel. The Liberian native has been hesitant to go beyond tribal boundaries. And the Americo-Liberians—settled along the coast and probably numbering about ten thousand—have mostly travelled to Europe and North America, where *Emilia* does not occur. Until the harbor at Monrovia was opened in 1948, coastwise steamers could not come in to shore along the Liberian coast. In contrast to Liberia, a dense human population in the Gold Coast and Nigeria, with consequent greater travel and more intensive agriculture, would explain the more frequent occurrence of this weed in those countries.

The flowers of *E. sonchifolia* fall within the purple-red color group. The color, approximating mallow pink, seems constant. Plants vary consider-

ably in size depending on conditions for growth. Our concept of the species, illustrated by Baldwin (1946), encompasses the type of *Cacalia sonchifolia* as well as that of *Cacalia lyrata;* those types were examined in the Linnaean Herbarium in London.

The following collections of *E. sonchifolia* were made:

Baldwin 5998 Liberia: Maryland Co.: Harper, June 14, 1947. *11219* Liberia: Grand Bassa Co.: Timbo, March 6, 1948. *11570* Liberia: Sinoe Co., Greenville, March 18, 1948. *11986* Ivory Coast: Abidjan, April 12, 1948. *11990* Gold Coast: Aburi: old botanical garden, April 17, 1948. *12525* Gold Coast: Accra: Achimota College, April 16, 1948. *11980* Nigeria: Agege (near Lagos): agricultural experiment station, April 28, 1948. *12524* Nigeria: Benin City: Oil Palm Research Station, May 3, 1948.

Baldwin likewise saw this species at Freetown, Sierra Leone, May 29, 1947.

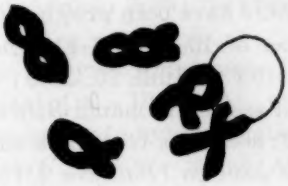
Seedlings represented by *Baldwin 11990, 12524,* and *12525* were grown, and their chromosomes studied by the junior author: $2n = 10$ (Accra material), $n = 5$ (Aburi material) (figs. 4–6). These results corroborate previous work.

At the Agege agricultural experiment station near Lagos, Nigeria, the senior author on April 28, 1948, collected specimens of *Emilia* which did not fit into the generic treatment of Hutchinson and Dalziel (1931) for West Africa: *Baldwin 11981.* The plants grew to a height of eighteen inches and had yellowish white corollas tipped with orange-red. Existence of these weeds at an agricultural station, which had been established in 1910, suggested the likelihood of accidental introduction there with seed of some economic plant.

Dr. S. F. Blake, relying on Garabedian's generic treatment, identified one of the Agege specimens as *E. sagittata* (letter of October 5, 1948). Dr. W. Robyns reported (letter of November 6, 1948) that the plant seemed to be *E. sonchifolia* var. *mucronata* Clarke and added (letter of December 15, 1948) that, though near *E. sonchifolia,* the Agege material matched no Brussels specimen exactly. Mr. E. Milne-Redhead (letter of December 20, 1948, from the Director, Kew) was unable to determine the Agege plant but found it to agree with two collections from Freetown, Sierra Leone, which, in his opinion, had been erroneously referred to *E. sagittata,* "a species from which they differ in having strongly toothed leaves, longer involucre bracts and pale yellow flowers."

FIGS. 1–10. Chromosomes of *Emilia.* FIGS. 1–3. *E. sagittata:* $2n = 10$ in leaf smear and $n = 5$ at diakinesis I and metaphase I of microsporogenesis. FIGS. 4–6. *E. sonchifolia:* $2n = 10$ in leaf smear and $n = 5$ at diakinesis I and metaphase I. FIGS. 7–8. *Emilia* sp.: $2n = 20$ in leaf smear and $n = 10$ at metaphase I. FIGS. 9-10. *E. coccinea:* $2n = 20$ in leaf smear and $n = 10$ at metaphase I. All figures × 2200.

1



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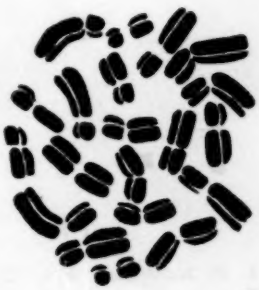

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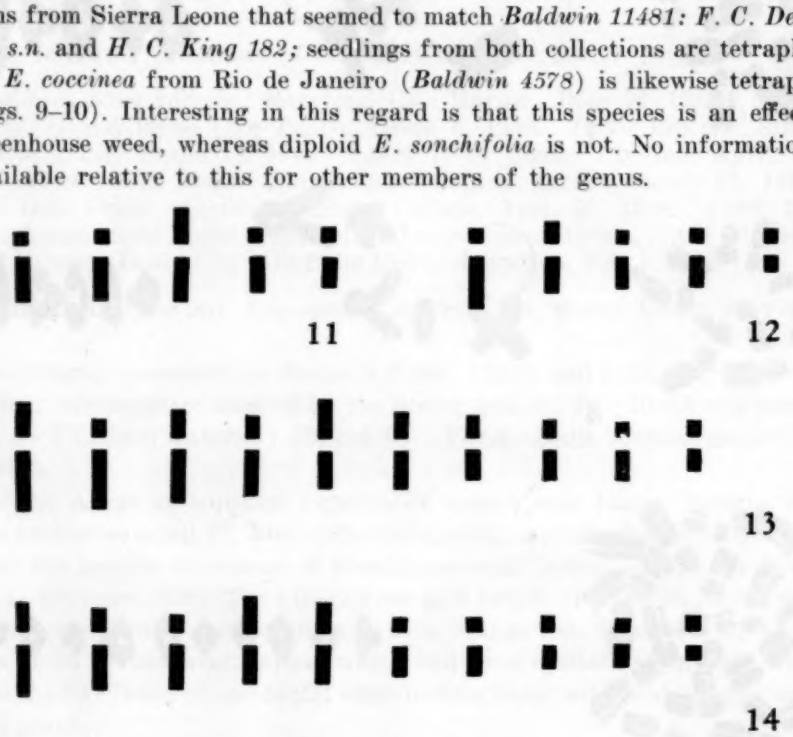
Seedlings of *Baldwin 11981* have been grown. Speese finds them to have a $2n$-number of 20, n-number of 10 (figs. 7–8). They are, therefore, tetraploid. E. Milne-Redhead (letter of June 20, 1949) sent seed of two collections from Sierra Leone that seemed to match *Baldwin 11481: F. C. Deighton s.n.* and *H. C. King 182;* seedlings from both collections are tetraploid.

E. coccinea from Rio de Janeiro (*Baldwin 4578*) is likewise tetraploid (figs. 9–10). Interesting in this regard is that this species is an effective greenhouse weed, whereas diploid *E. sonchifolia* is not. No information is available relative to this for other members of the genus.



FIGS. 11–14. Idiograms of *Emilia* chromosomes. FIG. 11. *E. sagittata.* FIG. 12. *E. sonchifolia.* FIG. 13. *Emilia* sp. FIG. 14. *E. coccinea.*

To determine whether or not chromosome morphology might afford data on phyletic affinities of the four *Emilia* representatives now cytologically known, idiograms of the chromosomes were made (figs. 11–14). Those idiograms demonstrate that neither the Agege plant nor *E. coccinea* is an autotetraploid of *E. sonchifolia* or of *E. sagittata.* No statement about affinities between the two tetraploids can as yet be given except to say that they do appear to have certain chromosomes in common and that under greenhouse conditions they somewhat resemble each other.

SUMMARY

Three representatives of *Emilia* occur in West Africa, and one plant (*E. guineensis*) is considered to have been erroneously referred to this genus. One representative of the genus is reported here for the first time as

an element of the West African flora; its proper designation has not been determined.

Mitotic and meiotic analyses were made for the three West African plants: two were diploid ($2n = 10$, $n = 5$), one tetraploid. Idiograms of chromosomes give no evidence of phyletic relations. But the tetraploid seems to have some affinity to *E. coccinea* which, as a tetraploid, is a tropical American weed and which is the only other cytologically known representative of the genus.

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THREE NEW SPECIES OF CHYTRIOMYCES FROM MARYLAND[1]

JOHN S. KARLING

The present contribution concerns three additional species of *Chytriomyces* which were discovered in the course of a survey of the soil fungi of Maryland. Members of this genus are characterized by monocentric encarpic thalli with extramatrical resting spores and operculate sporangia, intramatrical rhizoids which may or may not arise from a subsporangial apophysis, and zoospores which in most species swarm in a vesicle outside of the sporangium. The new species from Maryland have these general characteristics but differ specifically from the known members of the genus primarily by zoospore size, character of the rhizoids, presence or absence of an apophysis, and the structure of the resting spore.

The first of these species to be described parasitizes *Closterium rostratum* and is distinguishable primarily by its small zoospores. It is, accordingly, named *Chytriomyces Closterii*. The other two species are saprophytic and were isolated from soil and water and grown on cellulosic and chitinic substrata. One of these species is characterized by coarse, rigid, and stiff-looking rhizoids, smooth resting spores, and by unusually large hyaline refractive globules in the mature sporangia and zoospores which give them a strikingly refringent or glistening appearance. Because of the latter characteristic it is named *C. lucidus*. The other species has spiny to verrucose and echinulate resting spores, apophysate sporangia, and very bushy rhizoids. The latter give the thalli a distinctive bushy appearance, and for this reason it is named *C. fructicosus*.

Chytriomyces Closterii Karling, sp. nov. Fungus parasiticus. Sporangiis hyalinis, laevibus, non apophysatis, sphaericis, 5–25 μ diam., pyriformibus, 6–19 $\times$ 9–24 μ diam.; operculo apicali, 4–6 μ diam. Zoosporis sphaericis, 2–2.5 μ, diam., globulo refractivo hyalino, 0.4–0.6 μ diam.; flagello 9–12 μ longo. Sporis perdurantibus hyalinis, laevibus, sphaericis, 7–12 μ diam., aut ovalibus germinantibus zoosporangia tenui membranata superficialia generentibus.

Sporangia hyaline, smooth, non-apophylate, spherical, 5–25 μ, or broadly pyriform, 6–19 $\times$ 9–24 μ, with one apical exit papilla; operculum shallow saucer-shaped, 4–6 μ diam., non-persistent. Zoospores spherical,

[1] This study was begun at the Chesapeake Biological Laboratory, Solomons, Md., where the writer was guest investigator during the spring and early summer of 1948. The author is very grateful to the Department of Research and Education, State of Maryland, and particularly to the Director of the Laboratory, Dr. R. V. Truitt, for providing research facilities and funds for this work.

2–2.5 μ, with a minute, 0.4–0.6 μ, hyaline refractive globule; flagellum 9–12 μ long; swarming actively in a vesicle outside of the sporangium. Single rhizoidal axis attached at base of sporangium, sparsely branched and sometimes extending for a distance of 120 μ. Resting spores hyaline, smooth, 7–12 μ, or oval with a large central globule surrounded by several smaller ones; content emerging through a pore in the wall during germination and forming a superficial sporangium.

Weakly parasitic on *Closterium rostratum* from a ditch along road to Drum Point Beach, Calvert County, Md.

Chytriomyces lucidus Karling, sp. nov. Fungus saprophyticus. Sporangiis hyalinis, laevibus, non-apophysatis, subsphaericis, aut elongatis, 18–44 × 28–66 μ diam., aut reniformibus; operculo apicali, 4–8 μ diam., hypocrateriformi demum evanescenti. Zoosporis ovalibus, 5.8 × 6.2 μ diam., globulo refractivo hyalino, 3.6–3.9 μ diam. Hyphis rhizomorphis ramosis, crassiusculis, 4–12 μ diam. Sporis perdurantibus hyalinis, laevibus, ovalibus aut elongatis, 15–18 × 20–25 μ; germinatione ignota.

Sporangia hyaline, smooth, non-apophysate, usually flattened and elongated transversely to rhizoidal axis, 18–44 × 28–66 μ, often almost hemispherical, or reniform, with one low, 3–4 μ high by 6–15 μ broad, apical exit papilla; operculum very shallow saucer-shaped, 4–8 μ diam., usually non-persistent. Zoospores slightly oval, 5.8 × 6.2 μ, with a large hyaline, spherical, 3.6–3.9 μ, refractive globule. Rhizoids coarse, rigid and stiff-looking, main axes 4–12 μ in diam., often extending for a distance of 400 μ and becoming thick-walled with age. Resting spores hyaline, smooth, oval, slightly elongate, 15–18 × 20–25 μ, with numerous angular refractive bodies; germination unknown.

Saprophytic in cellulosic substrata in soil and water along road to Drum Point Beach, Md.

Chytriomyces fructicosus Karling, sp. nov. Fungus saprophyticus. Sporangiis hyalinis aut subfuscis, laevibus, plerumque apophysatis et appendiculatis, subsphaericis, 17–35 μ diam., aut ovalibus, 31–42 × 37–50 μ diam., aut hemisphaericis, 15–55 μ diam., aut pyriformibus, aut obclavatis, aut citriformibus, aut elongatis; 1–2 papillis aut tubulo, 8–12 × 10–60 μ, exeuntibus; operculo 4–8 μ diam., evanescenti. Zoosporis ovalibus, 3.8–4.2 × 5.5–6 μ diam., globulo refractivo hyalino, 1.2–1.8 μ diam. Apophysis sphaericis, 8–20 μ diam., fusiformibus 14–16 × 20–30 μ, irregularis, aut angularibus. Hyphis rhizomorphis fructicosus, crassiusculus, 3–8 μ diam., aut tenuissimis. Sporis perdurantibus subfuscis, spinosis aut verrucosis, sphaericis, 18–30 μ diam., aut ovalibus, aut angularibus; germinatione ignota.

Sporangia hyaline to light brown, often appendiculate and usually apophysate, variable in size and shape, almost spherical, 17–35 μ, oval, 31–42 × 37–50 μ, almost hemispherical, 15–55 μ diam., broadly and narrowly pyriform, obclavate, citriform, elongate, or slightly anatropus, with 1–2 low exit papillae or 1–3 tapering exit tubes, 8–12 μ broad at the base by 10–60 μ long. Operculum saucer- to bowl-shaped, 4–8 μ diam., non-persistent. Zoospores oval, 3.8–4.2 × 5.5–6 μ, with a hyaline, spherical, 1.2–1.8 μ, refractive globule; swarming actively and briefly in a vesicle outside of the sporangium. Apophysis variable in size and shape, rarely spherical, 8–20 μ,

oval, 8–15 × 20–25 μ, fusiform, 12–15 × 27–30 μ, elongate, 18–20 × 30–32 μ, irregular or angular. Rhizoids bushy in appearance and frequently branched, angles of branching obtuse and frequently at right angles; main axes centered on the base of the apophysis or arising at several points on the periphery, 3–8 μ in diam., branches occasionally extending for a distance of 275 μ. Resting spores light amber to greenish brown, usually spiny, occasionally verrucose or echinulate; spines up to 15 μ long by 3 μ wide at base; spherical, 18–30 μ, including spines, oval or slightly angular, with finely granular content; germination unknown.

Saprophytic on chitinous substrata in soil and water along route 505, Calvert County, Md.

CHYTRIOMYCES CLOSTERII. This species occurred in a collection of *Draparnaldia glomerata* and other algae which were brought into the laboratory on March 31, 1948. It does not appear to be a virulent parasite because it usually attacked *Closterium rostratum* only after this desmid had been kept in the laboratory for several days and become moribund. However, in a few cases healthy desmids were attacked and killed. So far it appears to be limited in host range to *C. rostratum*. It was never found to attack other species of *Closterium*, *Spirogyra*, *Mougeotia*, *Oedogonium*, *Vaucheria*, *Stigeoclonium*, or *Draparnaldia glomerata* which were growing in the same dishes with the parasitized *C. rostratum*.

In exceptional cases as many as 20 parasites may be found on a single host cell, but in most instances only 1–9 parasites are present (fig. 1). The parasite does not cause any enlargment or malformation of the host cell as in the case of *Chytriomyces parasiticus* (Karling 1947a). However, as the rhizoids elongate and branch the chloroplast, starch grains, and other parts of the protoplasm became clumped around them (fig. 1). Eventually, a large portion of the protoplasm is absorbed, while the remainder degenerates.

Of the known species of *Chytriomyces*, *C. Closterii* resembles *C. parasiticus* most closely by its small thalli, but it differs specifically from this species by its smaller zoospores (fig. 2), lack of an apophysis, and more extensive rhizoids. The latter may often be filled with refractive globules. In other respects, structure, and method of development, *C. Closterii* is fundamentally similar to other species of *Chytriomyces* and need not be described further.

CHYTRIOMYCES LUCIDUS. This species developed on small bits of onion skin, grass leaves, and to a limited extent on cellophane, but so far it has not grown on chitin. It is distinguished primarily by its large zoospores (fig. 13) which contain an unusually large refractive globule, very stiff and rigid-looking rhizoids (fig. 6), and by hyaline, smooth resting spores (figs. 15–17). Its zoospores are approximately the same size and shape as those

of *C. appendiculatus*, but the included refringent globule is usually twice as large. The size of the globules is such that in mature sporangia they appear to be packed together with very little space between them (figs. 6–10), which gives the sporangia a brilliant refractive appearance.

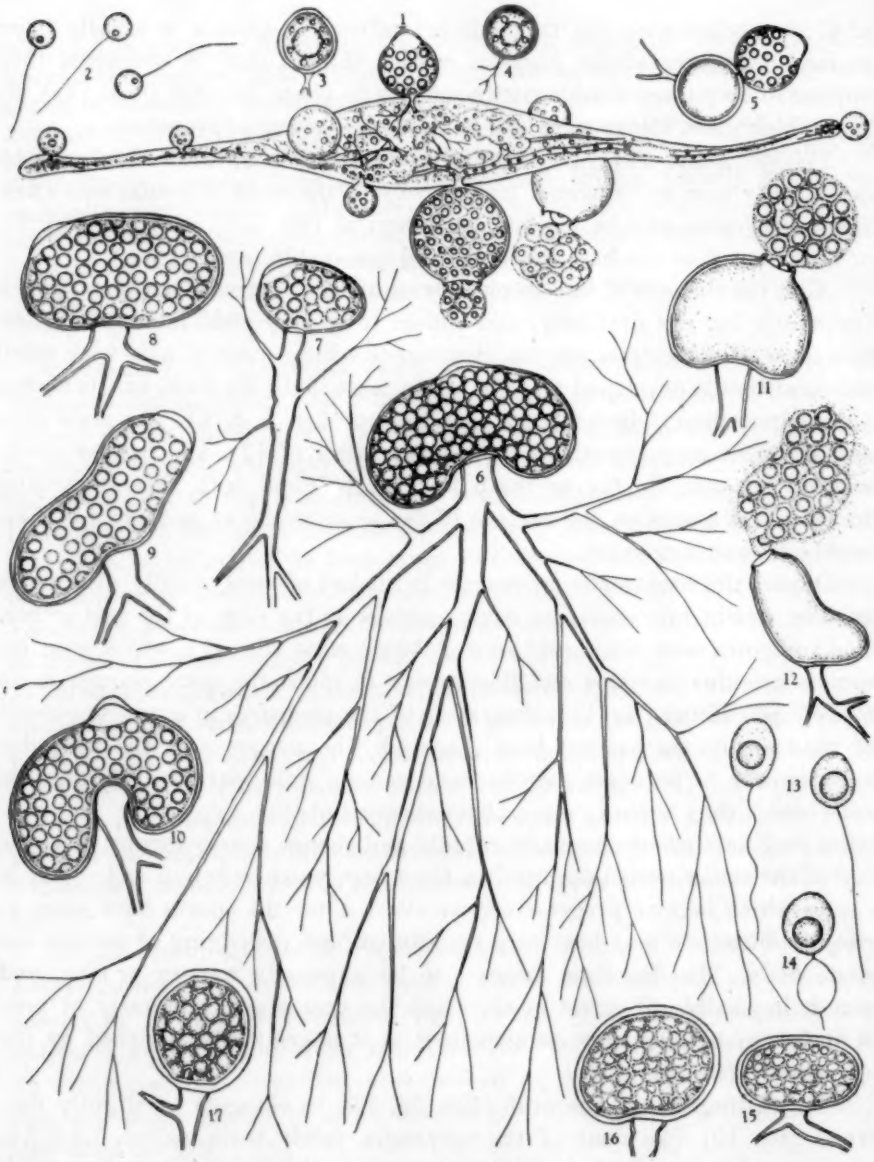
The sporangia may vary markedly in size and shape, but they are predominantly oval or elongated transversely to the main rhizoidal axis (figs. 7–9). They may also be almost hemispherical (fig. 11), reniform (fig. 6), or invaginated at the base (fig. 10), and nonapophysate.

Also, the rhizoids of this species are rather distinctive. They may branch frequently but not profusely, and appear to be very rigid and stiff (fig. 6) like those of *Rhizidium* species. Sometimes a large central axis with small side branches is developed (fig. 7), but in most thalli the main axis branches almost immediately beneath the sporangium (figs. 6, 8, 9). The main axes and branches may sometimes attain a diameter of 12 μ and become thick-walled with age. So far no thalli have been found with rhizoids arising from several points on the surface of the sporangium as in species of *Rhizophlyctis* and *Karlingia*.

During dehiscence the operculum is pushed off and usually disappears quickly, but in rare instances it may persist at the edge of the exit orifice. The zoospores ooze out slowly in a globular mass (fig. 11), which soon becomes irregular in shape and floats away in much the same manner as in *C. appendiculatus* (fig. 12). Swarming of the zoospores in a vesicle outside of the sporangium has not been observed. The zoospores in the irregular mass appear to be stuck together and remain quiescent for 1–2 minutes, after which they begin to move about slowly and then swim away. In swimming they dart about unusually rapidly and change course abruptly. As the end of the motile period approaches, the zoospores swim round and round in circles which become progressively smaller. After the spores have come to rest, the flagellum may beat very rapidly without dislodging or moving the spore body. The flagellum appears to be unusually narrow or fine, and almost impossible to detect or see until the spores are completely at rest. A vesicle or vesicles may develop in it as it is gradually absorbed by the spore body (fig. 14).

The resting spores are oval (figs. 16, 17) to elongate or slightly flattened (fig. 15) like some of the sporangia, fairly thick-walled, 1.5–2.3 μ, hyaline and smooth, and contain numerous angular refractive bodies which are usually closely packed together. The rhizoids on these spores are almost as extensive and thick-walled as those on the sporangial thalli.

CHYTRIOMYCES FRUCTICOSUS. This species grows well only on purified chitin and is, accordingly, chitinophilic. Its most striking characteristics are the bushy, bristly, and stiff-looking rhizoids which usually arise from

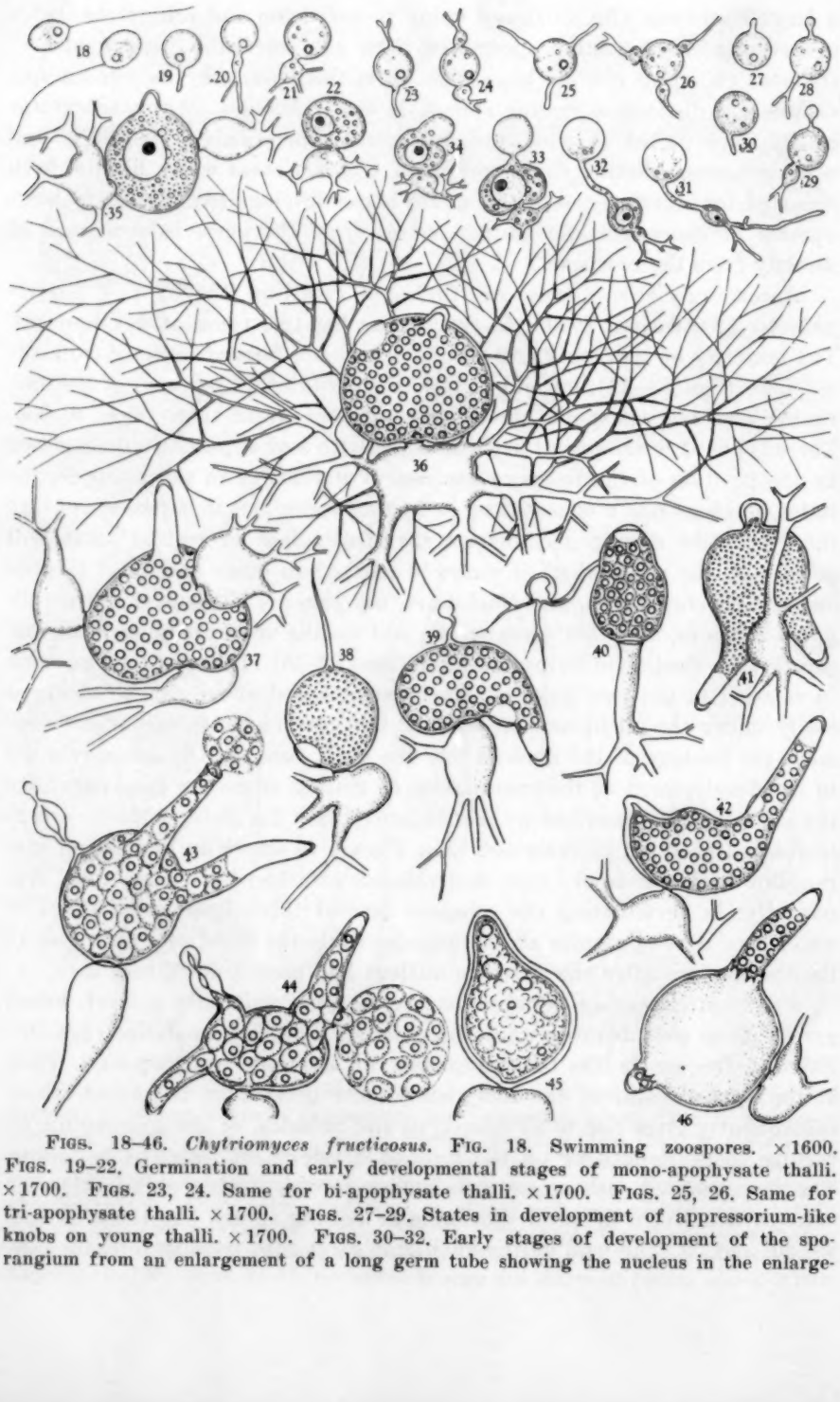


FIGS. 1–5. *Chytriomyces Closterii.* FIG. 1. *Closterium rostratum* infected with 9 parasites in various stages of development and maturation. ×1400. FIG. 2. Swimming zoospores. ×1600. FIGS. 3, 4. Mature resting spores. ×1400. FIG. 5. Germinating resting spore. ×1400. FIGS. 6–17. *Chytriomyces lucidus.* FIG. 6. Mature thallus with stiff- and rigid-looking rhizoids and reniform sporangium filled with large refringent globules. ×1400. FIGS. 7–10. Variations in shapes and sizes of sporangia. ×1400. Fig. 11. Dehiscing sporangium. ×1400. FIG. 12. Discharged mass of zoospores floating away. ×1400. FIG. 13. Swimming zoospores. ×1700. FIG. 14. Zoospore with vesicle in flagellum. ×1700. FIGS. 15–17. Variations in sizes and shapes of resting spores. ×1400.

a large apophysis (fig. 36), and spiny to verrucose and echinulate, light- or greenish-brown resting spores. In these characteristics it resembles *C. stellatus* (Karling 1947a), but differs from this species by its smooth sporangia and distinctive resting spores. It also resembles *C. appendiculatus* by its thick-walled rhizoids and numerous appendiculate sporangia and resting spores. Another characteristic of *C. fructicosus* which has not been reported for other species of this genus is the development of a fairly large number of sporangia and resting spores from the germ tube instead of directly from the zoospore.

Accordingly, like species of *Karlingia* (Karling 1947b) and *Asterophlyctis* (Antikajian 1949), *C. fructicosus* has two types of development. The majority of sporangia and resting spores are formed directly from the zoospore (figs. 19–22), but out of 200 thalli studied 18 per cent of the sporangia and resting spores developed from the germ tube (figs. 30–33). These types of development are associated with and apparently determined by the position of the zoospore nucleus. If it remains in the zoospore, the latter develops into a sporangium or resting spore, but if it passes out into the germ tube during germination the sporangium or resting spore will develop at the place where it comes to rest. As in other species of *Chytriomyces*, *Asterophlyctis*, and *Obelidium*, the primary nucleus of the germinated zoospore, incipient sporangium, and resting spores is quite large and can be seen readily in living material (figs. 32–35). Therefore, its position in relation to the two types of development noted above can be observed easily under the oil immersion lens. In the less frequent type of development the passage of the nucleus into the germ tube and its space relation to the development of the sporangium or resting spore are fundamentally the same as those described by Antikajian (1949) for *Asterophlyctis sacoptoides* and need not be described here. Figure 40 shows an interesting sporangium with a zoospore cyst, and rhizoids attached by a germ tube. Apparently, in germinating the zoospore formed three basal germ tubes of which two developed into short rhizoids, while the third one gave rise to the sporangium after the zoospore nucleus had passed down into it.

Fairly often during germination the zoospore will form a short, broad germ tube or protuberance whose tip enlarges to become knob-like (figs. 27–29) and frequently has the appearance of a minute appressorium. Then at the opposite side of the zoospore another germ tube is formed which subsequently gives rise to an apophysis and rhizoids, or the sporangium or resting spore, depending on the type of development which is to follow. The formation of such appressoria-like structures during germination results eventually in knobbed sporangia or resting spores like those in figs. 39, 50, and 52. The wall of the knob and germ tube usually thickens con-



FIGS. 18–46. *Chytriomyces fructicosus.* FIG. 18. Swimming zoospores. ×1600. FIGS. 19–22. Germination and early developmental stages of mono-apophysate thalli. ×1700. FIGS. 23, 24. Same for bi-apophysate thalli. ×1700. FIGS. 25, 26. Same for tri-apophysate thalli. ×1700. FIGS. 27–29. States in development of appressorium-like knobs on young thalli. ×1700. FIGS. 30–32. Early stages of development of the sporangium from an enlargement of a long germ tube showing the nucleus in the enlarge-

siderably (figs. 43, 44) and in some cases they are solidly composed of wall material and very stiff or rigid looking.

As noted in the diagnosis above and shown in figures 35–39, the apophysis of this species is very large, conspicuous, and variable in shape. Some thalli may have two apophyses (fig. 35), and in rare cases three (fig. 37). They begin as local enlargements of the germ tube (figs. 20, 21), and in instances where the zoospore forms two or three germ tubes a similar number of apophyses may develop (figs. 23–26). Thus, at maturity they may be located at opposite sides or almost equidistant on the surface of the sporangium (fig. 35, 37) or resting spore.

A few nonapophysate thalli have been found with rhizoids arising at two or three points on the sporangium, and such thalli may be strikingly similar in appearance to *Karlingia* species. However, the two may be distinguished by the presence of a large primary nucleus in the fully formed sporangia of *C. fructicosus* (fig. 35), which apparently is lacking in *Karlingia*. As has been reported previously (Karling 1947a) for other species of *Chytriomyces*, division of the primary nucleus is delayed until the sporangia and resting spores have attained mature size. In *Karlingia*, on the other hand, it apparently divides very early in development because the fully formed sporangia are multinucleate.

The sporangia of *C. fructicosus* also vary markedly in size and shape (figs. 35–44), and instead of exit papillae they may develop long tubes. In some cases both papillae and tubes are formed on the same sporangium. The tubes may be up to 60 μ in length and usually taper markedly from base to tip. However, they do not always function in the discharge of zoospores and may remain closed at the tip. Occasionally, the operculum fails to develop at the tip and may form at the side or base of the tube (figs. 39, 42, 44). In anatropous sporangia the necks may often extend down towards

ment. ×1700. FIG. 33. Same development from a short germ tube; nucleus clearly visible in incipient sporangium; zoospore case attached as an appendage. ×1700. FIG. 34. Development of sporangium from only a portion of zoospore case. ×1700. FIG. 35. Bi-apophysate, fully formed sporangium with large primary nucleus. ×1400. FIG. 36. Portion of a mature thallus showing the characteristic stiff-looking, bushy rhizoids. ×1400. FIG. 37. Tri-apophysate sporangium with short neck. ×1400. FIG. 38. Subspherical sporangium with a terminal unbranched rhizoid and a basal exit papilla. ×1400. FIG. 39. Knobbed, anatropus sporangium with short neck and basal exit papilla. ×1400. FIG. 40. Stalked non-apophysate sporangium which apparently developed from the germ tube; zoospore case with rhizoids attached at left. ×1400. FIG. 41. Appendiculate sporangium with two necks extending down towards apophysis. ×1400. FIG. 42. Sporangium with wall thickened at one end. ×1400. FIG. 43. Discharge of zoospores from a sporangium with two necks; appresorium-like knob and zoospore case attached at left. ×1200. FIG. 44. Zoospores swarming in a vesicle; exit tubes or necks non-functional. ×1200. FIG. 45. Dormant, thick-walled sporangium. ×1200. FIG. 46. "Germination" of thick-walled sporangium. ×1200.

the apophysis (figs. 39, 41). Sometimes the sporangia may become thick-walled and light brown in color and go into a dormant state as in *C. appendiculatus* (fig. 45). Then, when they form zoospores the exit papillae or tubes break through the thick wall (fig. 46).

During dehiscence the operculum is pushed off by the emerging zoospores and disappears quickly from view. The mass of zoospores is surrounded by a layer of matrix which expands as more and more spores are discharged. In a short time a delicate vesicle is formed in which the zoospores swarm actively for 1–2 minutes (fig. 44). When the vesicle ruptures, the zoospores dart out, but usually they do not swim far away. Instead, they frequently come to rest in groups and germinate, which results in the development of aggregates of sporangia or resting spores on the chitinous substratum. Germination of zoospores in situ occurs occasionally with the result that either sporangia or resting spores may develop within the old sporangium.

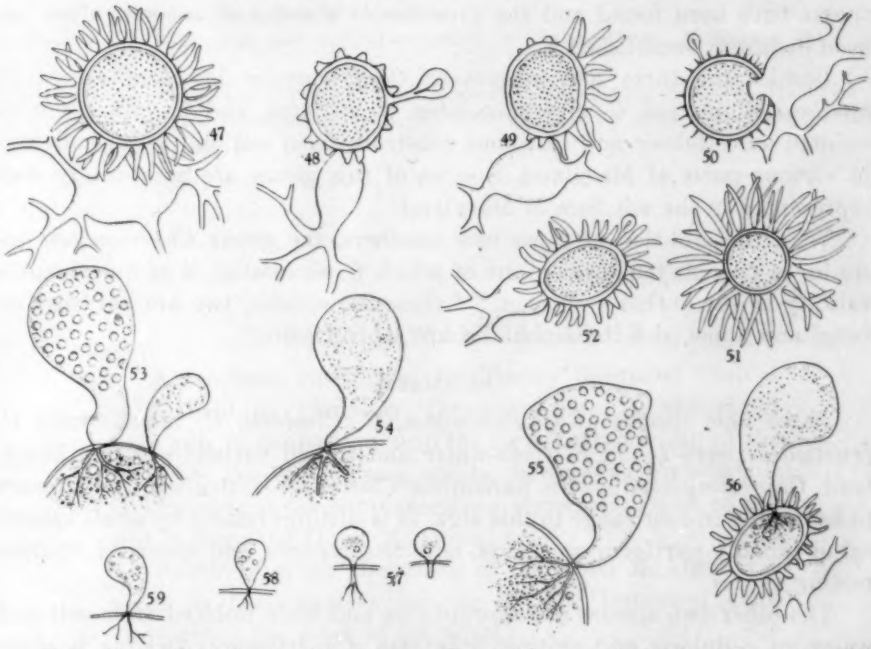
The resting spores develop directly from the zoospore (figs. 47, 49–52) or from an enlargement of the germ tube in the same manner as the sporangia described previously. In the latter type of development the empty zoospore cyst and germ tube may persist as an appendage to the spore (fig. 48) and usually become thick-walled. They frequently look like the male thallus and conjugation tube or canal which are attached to the resting spore of *Siphonaria*. Therefore, unless the developmental stages are studied carefully one might conclude that such resting spores in *C. fructicosus* have developed as the result of fusion of two thalli. The development of these spores is fundamentally similar to that described by Antikajian for *Asterophlyctis sarcoptoides*.

The spines or conical pegs on the spores vary from 22 to 70 per spore, taper gradually and may be up to 15 μ long in exceptional cases (fig. 51). The usual length is between 4 and 8 μ, with a width of 2.5–3.5 μ at the base. On some spores they may be reduced to warts (fig. 48) so that such spores are distinctly verrucose. Figure 49 shows an exceptional spore which is partly smooth, verrucose and spiny. Echinulate spores are rare (fig. 50) and so far no completely smooth ones have been found.

PARASITE OF C. FRUCTICOSUS. During the course of this study the sporangia and resting spores of *C. fructicosus* became parasitized by another small chytrid which possibly belongs in the genus *Rhizophydium*. Its sporangia are broadly obpyriform or clavate, 15–22 × 24–30 μ, with a tapering, curved base (figs. 54–56). The sporangia are quite broad at the apex, and in some cases they may be almost flat on top (fig. 55). The apical exit papillae are not prominent or conspicuous, and so far I have been unable to determine whether or not the sporangia are operculate. The rhizoids are intramatrical and branched, fairly short and broad in diameter, and

sometimes abruptly tapered. In a few sporangia observed, the rhizoids were reduced to digitate structures (fig. 54).

Whether or not this chytrid is an obligate parasite of *C. fructicosus* is not certain, but it may be noted here that it did not parasitize *Cladochytrium replicatum, Nowakowskiella macrospora, N. profusa, Chytriomyces hyalinus, Aphanomyces laevis,* and *Pythium* sp., which were growing in the same culture. In one instance it was found parasitizing the main rhizoidal



FIGS. 47–52. *Chytriomyces fructicosus.* FIG. 47. Large spherical resting spores with long tapering pegs or spines. ×1400. FIG. 48. Verrucose resting spore with zoospore case and germ tube at right. ×1400. FIG. 49. Partly smooth, verrucose and spiny resting spore. ×1400. FIG. 50. Echinulate spore with knob. ×1400. FIG. 51. Small spherical spore with unusually long spines. ×1400. FIG. 52. Knobbed, oval resting spore. ×1400. FIGS. 53–59. *Rhizophydium*-like parasite of *C. fructicosus.* FIG. 53. Mature and young sporangia with branched rhizoids. ×1400. FIG. 54. Curved sporangium with digitate rhizoids. ×1400. FIG. 55. Mature sporangium with flattened top. ×1200. FIG. 56. Parasitized resting spore of *C. fructicosus.* ×1400. FIGS. 57–59. Germination of zoospore and early developmental stages of thalli. ×1600.

axis of *C. fructicosus* where it caused a distinct enlargment or malformation. However, no malformations were noted in cases of infected sporangia. In such structures part of the protoplasm accumulates around the rhizoids of the parasite, while the remainder undergoes degeneration.

No resting spores of the parasite were observed. Therefore, it is impossible to classify or properly name this chytrid at present. Nevertheless, it should be noted here that its sporangia are somewhat similar in shape to

those of *Phlyctidium mycetophagum* (Karling 1946b) which parasitizes *Chytriomyces hyalinus, C. aureus,* and *C. appendiculatus* among numerous other chytrids. In the latter parasite, however, the rhizoid is unbranched and usually thread-like or filamentous, and the two species differ in this respect. The parasite of *C. fructicosus* is probably a member of *Rhizophydium* which includes parasites of *Chytriomyces* and other chytrid genera (Karling 1946a, c), but its identity will remain uncertain until its resting spores have been found and the presence or absence of an operculum has been definitely established.

Besides the three new species of *Chytriomyces* described above, *C. hyalinus, C. aureus, C. appendiculatus, C. stellatus,* and *C. spinosus* were isolated on cellulosic and chitinous substrata from soil and water collected in various parts of Maryland. Species of this genus are accordingly well represented in the soil flora of Maryland.

With the addition of these new members, the genus *Chytriomyces* includes at present ten species, one of which *C. nodulatus,* is of questionable validity in the author's opinion. Of these ten species, two are parasitic on fungi and algae, and the remainder are saprophytes.

SUMMARY

Three new species of *Chytriomyces, C. Closterii, C. lucidus,* and *C. fructicosus* were found in fresh-water and soil in various parts in Maryland. *Chytriomyces Closterii* parasitizes *Closterium rostratum* and appears to be limited in host range to this alga. It is distinguishable by small spherical or broadly pyriform sporangia, minute zoospores, and spherical, hyaline resting spores.

The other two species are saprophytes and were isolated from soil and water on cellulosic and chitinic substrata. *Chytriomyces lucidus* is characterized primarily by large zoospores with an unusually large refractive globule which gives them and the sporangia a glistening appearance, and by stiff-looking and bristly rhizoids, and hyaline, smooth resting spores. It was isolated and growing on bits of onion skin, and does not grow on chitinous substrata. In contrast, *C. fructicosus* is chitinophilic in relation to its substrata. It is distinguishable by its bushy rhizoids which arise from one or more apophyses, appendiculate sporangia, and spiny, greenish-brown resting spores. It was often found to be parasitized by another *Rhizophydium*-like chytrid.

In addition to these new species of *Chytriomyces, C. hyalinus, C. aureus, C. appendiculatus, C. spinosus,* and *C. stellatus* were ioslated from soil and water in various parts of Maryland.

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TORREY BOTANICAL CLUB

A luncheon meeting of the Torrey Botanical Club is to be held on Thursday, December 29th, at the Hotel McAlpin, in connection with the New York meeting of the A.A.A.S. Dr. W. H. Camp will be the speaker. Tickets will be available at the supplementary registration desk of the A.A.A.S. in the Hotel McAlpin.

Parlor B on the Mezzanine of the Hotel McAlpin will serve as headquarters for the Torrey Botanical Club throughout the week of meetings.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 76, NO. 5, PP. 364–373 SEPTEMBER, 1949

TORREYA

PROCEEDINGS OF THE CLUB

Minutes of the meeting of February 1, 1949. The meeting was called to order at 8:05 P. M. by President Matzke at Columbia University; 51 members and friends were present. Dr. B. O. Dodge of the N.Y.B.G. spoke on "Taxonomic and genetic features bearing on the origin of *Neurospora tetrasperma.*" Dr. Dodge's abstract follows:

The genus *Neurospora* was proposed by Shear & Dodge to include those species of the Sphaeriales having dark striated ascospores and orange-colored conidia borne on dichotomously branched sporophores. The perfect stage of the well-known bakery mold, or red bread mold, was named the type species. It appears that this mold was first mentioned in scientific literature in 1843, when Léveillé referred to it as *Oidium aurantiacum;* that same year Montagne described and illustrated it under the name *Penicillium sitophilum.* The authors of the new genus *Neurospora* discussed the systematic relations of the bakery mold to other Sphaeriales, but were unable to suggest whence it arose. As is to be expected, the fungus has been described under a number of different names; it appears that *N. sitophila* is the correct one.

There are six species of *Neurospora,* three of which have 8-spored asci; they differ in the dimensions of asci and ascospores. *N. crassa* seems to have somewhat smaller conidia, which are more pinkish in mass than those of other species. The other three Neurosporas have 4-spored asci which clearly differ in morphology. *N. Toroi* and *N. tetrasperma,* although they differ morphologically only slightly, cannot readily hybridize. While the accumulation of very small changes in an 8-spored species may have given rise to the first 4-spored one, such a type could have arisen suddenly by way of few macromutations; it seems unlikely that the first 4-spored species was ancestral to the others. Regardless of the manner of origin of species —whether by slight or large mutations—it seems certain that the 8-spored are ancestral to the 4-spored.

Evidence has accumulated suggesting that *N. tetrasperma* may have arisen directly from the *N. sitophila* type, even though these species differ in other respects than the number of spores. Asci of *N. tetrasperma* sometimes contain five spores, two smaller than the rest, and of the same size as those of *N. sitophila.* The small spores are so often at the lower, somewhat narrower end of the ascus that it seems likely that with reduction in diameter of the whole ascus the species would revert to 8-sporedness, or conversely that 4-sporedness may have become established in an originally 8-spored species as a result of broadening and shortening of the ascus.

Some ten years ago the discovery was reported of a heterocaryotic race of *N. tetrasperma* in which nuclei of one mating type carry a lethal gene, those of opposite type being normal. This lethal has three distinct effects: 1. On corn-meal agar the heterozygous *E/e* asci usually aborted without delimiting spores. 2. In the occasional instances when the lethal did not cause abortion the asci produced eight small spores instead of the four large ones characteristic of the species; the small spores were indistinguishable from those of *N. sitophila.* 3. The lethal factor was shown to be in-

herited according to a simple Mendelian ratio: four of the ascospores carried a single *E* nucleus, and four the normal *e*. Those carrying the lethal *E* often germinated but on corn-meal agar soon died; the other four developed normally. An occasional ascus was 7-spored; the giant spore was heterocaryotic for mating-type and for the lethal. By propagating vegetatively by transplantation the original heterocaryon has been preserved for 10 years. By propagating from the large spores it was possible to carry the lethal from generation to generation through the sexual phase of reproduction; from the small normal *e* spores came only the normal *N. tetrasperma* with four large spores.

The reversion from the 4-spored to the 8-spored type was then only a temporary one; at the first opportunity the lethal is eliminated. Recent work has been directed to the problem of carrying the lethal through to growth into functional mycelia. By plating out the conidia from heterocaryotic (*E*/*e*) mycelium and selecting the smallest and most abnormal germinating conidia for transfer to a special agar, several races pure for the lethal were obtained. The culture medium was a potato-dextrose agar in which the potato decoction was made from new or half-grown potatoes. It was of course necessary to test the isolates for purity. Several of the mycelium gave rise to 8-spored asci, and were therefore shown to carry *E*.

The new-potato-steep dextrose medium which was potent to prevent ascus abortion was found to be potent to a certain extent to prevent the death of ascospore germlings. In this way it has been possible to obtain 31 races pure homocaryotic for the dominant lethal *E* which will grow and function in sexual reproduction when mated with normal *e* tester-races of *N. tetrasperma*.

The next step is to obtain races of both mating types carrying the lethal *E*. From such races could be obtained asci homozygous for *E*, and ascospores all carrying the lethal. Along with the strain of opposite mating-type must be discovered an agar on which the life cycle can be carried to completion. The reversion from 4-sporedness in *N. tetrasperma* will then be permanent. The resulting fungus will still not be *N. sitophila*, since the species differ in other characters. But in the most significant respect, spore-number, the first step in permanent reversion has been accomplished.

After lively discussion of the address, the meeting was adjourned at 9:25.

Minutes of the meeting of March 16, 1949. After refreshments served by members of the University, the meeting was called to order at 4 P.M. by President Matzke at Fordham University; 58 members and friends were present. The minutes of the preceding meeting were read and approved. Dr. Charles Berger spoke on "Recent botanical research at Fordham." Dr. Berger's abstract of his address follows:

> Another case of the natural occurrence of polyploid cells in the development of a diploid plant has been found in the silktree, *Albizzia julibrissin*. Several interesting differences between the phenomenon as it occurs in *Albizzia* and in two previously reported cases were described.
>
> A new case of endomitosis in the tapetal cells of the snapdragon *Antirrhinum majus* was also reported. Some of the tapetal cells undergo two successive endomitotic divisions which may be followed by a normal mitotic division of the polyploid cells.

Afterwards time-lapse phase-contrast microcinematographs were shown of the process of meiosis. No further business was transacted. The meeting was adjourned at 5:10.

Minutes of the meeting of April 5, 1949. The meeting was called to order at 8:10 P. M. by President Matzke at Columbia University; 37 members and friends were present. The minutes of the preceding meeting were read and approved.

The following names were presented for election to membership: Life Member: L. J. Gier, Liberty, Mo. Active Members: Mrs. Gily E. Bard, New Brunswick, N. J.; Clarke Q. Brown, Caldwell, Idaho; Percy Camp, Toms River, N. J.; Mrs. Percy Camp, Toms River, N. J.; Allan P. Chan, Ottawa, Canada; Mavin S. Dunn, Lansdowne, Pa.; Robert C. Frohling, Union, N. J.; A. S. Heiba, Tucson, Ariz.; Doris Holtzman, Brooklyn, N. Y.; Jeanette M. Dryn, Buffalo, N. Y.; Jose V. C. Malato Beliz, Elvas, Portugal; Harold McIlvaine, Moscow, Idaho; Marion R. Myles, Nashville, Tenn.; Lindsay S. Olive, New York, N. Y.; Elsie Phelon Phillips, New York, N. Y.; Harry K. Phinney, Corvallis, Ore.; H. W. Popp, State College, Pa.; W. C. Price, Pittsburgh, Pa.; B. A. Razi, Bangalore, India; Donald D. Ritchie, New York, N. Y.; S. B. Shively, Lincoln, Nebr.; Edward E. Terrell, Ithaca, N. Y.; Sylvia White, Washington, D. C.; John L. Wood, Mont Alto, Pa. Associate Members: Charles Bell, Lower Bank, N. J.; Marie E. Boyle, Bryn Mawr, Pa.; Harold E. Clark, New Brunswick, N. J.; Ruth Goodman, New York, N. Y.; Richard D. Ilnicki, Jamesburg, N. J.; William P. Jacobs, Princeton, N. J.; Gordon N. Murray, Martin, Tenn.; Kathleen Prestwidge, New York, N. Y.; Anne O. Seaman, New York, N. Y. All were elected.

Dr. Zimmerman announced, for the committee to find a successor to Dr. Rickett as editor of the Bulletin, that Dr. Rickett's resignation had been accepted and Fr. Berger elected to that post by the Council. It was unanimously voted that the thanks of the Club be extended to Dr. Harold Rickett for his long, faithful, and successful service as editor.

The committee for the Andrews Research Fund reported that the following grants for research had been made from the Fund: Dr. Richard Goodwin, $300; Dr. Robert Clausen, $250; Brother Leon, $150; Dr. Charles Heimsch, $250.

Dr. Richard Goodwin of Connecticut College discussed his "Studies on the fluorescence of roots." His abstract follows:

> The tissues of plants when placed in ultraviolet light are likely to exhibit fluorescence as a result of the presence of fluorescing organic compounds within the cells. Green tissues exhibit a red chlorophyll fluorescence which is so bright that the fluorescence of other compounds is likely to become obscured. The fluorescence of these other compounds can be observed more clearly in non-green organs such as roots.
>
> The speaker wishes to acknowledge the collaboration of Dr. Frederick Kavanagh in the work which is being reported. The roots of 135 species of vascular plants, representing 69 families, have been examined in ultraviolet light. Of these, all but six species of ferns with much dark pigment in the roots exhibited fluorescence. The color of the fluorescence was most frequently blue, bluish, or bluish-white, but was sometimes greenish, greenish-yellow, or red. The fluorescing substances have been extracted with acetone and with n-butanol from the roots of nine different species, including three of the above-mentioned ferns. The blue-fluorescing material extracted from *Avena sativa* roots has been separated into at least three distinct fractions which can be distinguished by their partition between immiscible solvents, by their adsorption on chromatographic columns, and by the intensity of their fluorescence over a wide range of acidity.
>
> One of these fractions has been identified as the coumarin derivative scopoletin, by comparing the pH-fluorescence curve and the ultraviolet ab-

sorption spectrum of the extract with that of a pure sample of scopoletin. Scopoletin is present in the mature portions of five-day-old *Avena* roots in concentrations in excess of 5×10^{-5} molar. From 3 to 18 mm. behind the root apex the amount of scopoletin was found to lie between 0.75 and 1.5×10^{-9} g., while in the apical 3 mm., which includes the meristem and region of cell elongation, the amount was too small to measure but was certainly less than 0.08×10^{-9} g. Recent studies have shown that coumarin derivatives and other compounds having an unsaturated lactone structure have growth-inhibiting properties, and it has recently been suggested that this may be tied in with the inactivation of sulfhydryl-containing enzymes. Whether scopoletin acts as a natural growth regulator is not known, but the fact that it is present in mature portions of *Avena* roots at concentrations high enough to inhibit growth while it is practically absent from the growing tip is suggestive.

After discussion the meeting was adjourned at 9:30.

Respectfully submitted,
DONALD P. ROGERS,
Recording Secretary.

FIELD TRIP REPORTS

April 3, 1949. The Pine Barrens and Plains of New Jersey. The main purpose of the trip was to view the broom crowberry (*Corema Conradii*) in flower. The season being somewhat advanced, only scattered blossoms remained. The station near Sim's Place was still healthy and vigorous. It is safe to say that on the West Plains acres of the crowberry are in good condition. The trailing arbutus (*Epigaea repens*), pyxie moss (*Pyxidanthera barbulata*), and sand myrtle (*Dendrium buxifolium*) were in bloom on the Plains and even a few early blossoms of the pine barren heather (*Hudsonia ericoides*) appeared.

April 14–16. Knoxville, Tennessee. Apparently no Torreyites attended the Knoxville meeting. At least no reports have reached the field chairman.

April 17. Pelham Bay Park, New York City. The group left for the Park at 10:15 A.M. The weather was clear but with a cool wind blowing. Very few spring flowers were noted and the marine flora does not usually appear until late spring. At the start of the trip the following marine algae were seen: *Enteromorpha intestinalis, E. Linza, Asperococcus echinatus, Fucus vesculosus, Ulva lactuca,* and at least two species of *Polysiphonia.* Other marine algae were noted but not identified. A rather rare shrub, *Amelanchier oblongifolia* var. *micropetala,* a dwarf juneberry, was observed coming into leaf where growing in crevices of rocks on the shore at the northern part of the Park. Attendance 10. Leader, William Rissanen.

April 17. Farmingdale, N. J. Eight members reported for this trip and as there were five cars we could have welcomed members by train. A walk along the railroad showed several plants though nothing startling but the river bottom along the Manasquan was yellow with *Caltha.* We seemed to disturb the trout fishermen there.

In the park area at Allaire, *Dicentra Cucullaria* had not yet reached its prime but many blossoms were out. *Viola scabriuscula* was abundant.

We visited the old ruins and found many cars there before us. Public interest seems to have awakened in the new state park. It is to be hoped that the flora does not suffer its usual fate in parks. Leader, Vernon L. Frazee.

April 24. Lakehurst, N. J. Rain failed to dampen the spirits of the group that assembled at the railroad station, and the Torrey group was soon joined by two carloads

of students and professors from Bucknell University, who were on the last lap of a four-day field trip.

The single bald cypress (*Taxodium distichum*) that persists at Lakehurst was visited first. High-bush blueberry (*Vaccinium corymbosum*) was flowering in abundance, as was pyxie moss (*Pyxidanthera barbulata*), sand myrtle (*Dendrium buxifolium*), shadbush (*Amelanchier canadensis*), black chokeberry (*Aronia nigra*), and bird-foot violet (*Viola pedata* var. *linariloba*). Although Lake Haricon at Lakehurst was being cleaned up a bit and most of the water drained off, the golden club (*Orontium aquaticum*) was everywhere in the upper stretches of mud covered lake bottom. The lance-leaved white violet (*Viola lanceolata*) grew along the shores and tiny, newly-formed leaves of the three species of sundews were just unfolding. Buds of the pitcher plant (*Sarracenia purpurea*) were beginning to form. Forays to nearby areas yielded several additional species. Ridgeway produced beautiful pink blossoms of the trailing arbutus (*Epigaea repens*); Colliers' Mills, the field pansy (*Viola Rafinesquii*); and Van Hiseville, budding blue lupine (*Lupinus perennis*). The highlight of the day came at its close. The members and guests remaining at dusk were shown the breath-taking beautiful swamp pink (*Helonias bullata*) near Allaire by Mr. Vernon Frazee who had known of the station since his youth. It left a very pleasant and lasting impression upon those viewing it for the first time. Attendance 20. Leader, David Fables.

April 30. Inwood Hill Park, N. Y. Ten Torrey members and guests joined in the botanical trip to Inwood Hill Park in the northwestern corner of Manhattan Island.

J. K. Small, in an article entitled "The Jungles of Manhattan Island—II" (Jour. N. Y. Bot. Gard. **38**: 308–316. 1937) listed the trees and shrubs of the area. A careful survey of Inwood Hill would certainly discover many additional species not noted by Small. These might serve as the subject of a short supplement, which would be not only interesting in itself but also, in a retroactive way, enhance the value of Small's census. For instance, the deerberry and the lowbush blueberry were listed by Small, but not *Vaccinium corymbosum* and *V. atrococcum* observed by the group. On the top of a hill was seen *Lyonia mariana*, which the writer first noticed there in 1936. Small listed the flowering dogwood, but missed *Cornus racemosa* (*C. paniculata*). We stopped to examine this species because of its peculiar leaf-scars which are deciduous in the springtime like those of *Hamamelis*. *Cornus rugosa* (*C. circinata*) is quite rare in the area, and Small's oversight of it is understandable. We suspect that the introduction into Inwood Hill Park of *Rubus phoenicolasius* and *Ribes sativum* (the common *R. vulgare* of manual, the anther-sacs being separated by a broad connective) must have antedated Small's study, but these two were missed.

Small's paper dealt with only the woody plants. It should be profitable to publish on the herbacious flora of Inwood Hill Park. This park and Fort Washington Park are the only two remaining wild areas of appreciable size in Manhattan, and a complete list of their plants would have historical interest not far in the future.

The Torrey Botanical Club noticed quite a number of flowers on the April 30th trip. Especially attractive were large colonies of *Dentaria diphylla* and *Alliaria officinalis*. On the east face of an old stone wall grew a beautiful cover of *Linaria Cymbalaria*. The writer has seen the kenilworth ivy on the same mossy wall since at least 1933, the same miniature violet dragonheads, two yellow spotted in front and sharp spurred behind. A close group of *Podophyllum peltatum* formed a low continuous canopy of shield-shaped leaves, which when lifted revealed the large white waxy flowers, nodding and richly fragrant. In the center of each blossom sat the plump pistil capped with its thick intricately undulate stigma; beneath, the pedicel showed minute streaks of ruby. The number of stamens varied. According to the Manual the number of stamens should be twice the number of petals. In two flowers bearing 6 petals we counted 10 stamens, one being very much reduced, and 17 stamens, four being much reduced.

Another interesting observation for the Torrey group was the seedling habit of *Acer pseudoplatanus*. Notwithstanding its dicotyledonous classification, specimens were ob-

served with three and four cotyledon-leaves in a whorl, and sometimes two with one deeply cleft. Judging from the nervature, the bilobed form is apparently best interpreted as two partly united cotyledons.

On the way out of the park, near the end of our trip, we saw along the walk a plantation of *Quercus ilicifolia*. The many dangling catkins presented an unusual and especially charming effect, being almost at eye level because of the scrub habit of the oaks.

It is recommended that the trip be repeated next year and a detailed list be kept of the species seen. Leader, Joseph Monachino.

May 20–22. Branchville, N. J. The thirty-fifth annual nature conference was held as sheduled. All but one of these sessions have been held at Branchville. During wartime restrictions on travel the Summit Nature Club took us to Watchung Reservation for the conference in 1945. For three seasons, during a change of management at The Pines, we were guests at The Haltere Hotel on Culvers Lake and this year an overflow of thirty-five participants were quartered there. A very interesting geology tour of Sussex County included outcroppings of rocks of various ages. An old rock (Oriskany limestone) but a recent habitation (Indian shelter) was seen at Bevans. This has been rereproduced as a habitat group in the State Museum at Trenton. A botanical excursion was made to Tillman Ravine in Stokes Forest and much botanizing was done around the hotel. Several species were added to the permanent list of plants: Peziza sp., Fissidens sp., *Adlumia fungosa, Angelica atropurpurea, Gaylussacia baccata* (thought to be a correction of the previously reported *G. dumosa*), and *Thalesia uniflora* (*Orobanche* in Gray's Manual). A large quantity of *Marsilea quadrifolia* was found on the small lake back of the hotel. This apparently brings to 617 the number of complete identifications from the region This list, corrected to 1948 may be obtained from Dr. H. N. Moldenke, New York Botanical Garden. The bird list ran to 105 species. Evening lectures on the above subjects were held as usual. Attendance 123, from 5 states. Leaders: David Fables, Louis Hand, James Hawley, Henry Herpers, Jr., Wallace Husk, Mr. and Mrs. C. B. Schaughency, Edgar T. Wherry.

Review and Discussion

Introgressive Hybridization. By Edgar Anderson. ix + 109 pages. *Pl. 1–5; fig. 1–23.* John Wiley & Sons, New York. 1949. $3.00.

Within the next year biologists will be celebrating the semicentennial anniversary of the rediscovery of Mendel's laws of inheritance. Yet, during this half-century of rapid advance in our knowledge of inheritance in living things, taxonomy in general has remained aloof from genetic concepts. For the most part its devotees have proceeded as if genetic phenomena were not present "in nature" but occurred only under the so-called controlled conditions of the breeder. Dr. Anderson's little book should go far in dispelling this common misconception regarding one facet of our knowledge concerning the genetic structure of the natural population.

The great multiplication of infraspecific names within recent years is clear evidence that taxonomists are beginning to discover the variability so characteristic of many of the taxa designated by them as species. Perhaps out of modesty the originator of the term "Introgressive Hybridization" has refrained from pointing out too forcibly that, to a large extent, this common phenomenon is the cause of much of the complexity which is confounding classical taxonomists and driving them to excessive nomenclatural tinkering.

The fact of widespread introgressive hybridization and consequent gene flow must be faced by the taxonomist if he is to bring to his studies any semblance of reality. The futility of attempting to jam the wide variability of such populations into relatively few named categories, or the equal absurdity of attempting to be logical and give all the variants "adequate" nomenclatural treatment by the recognition of a large series of named taxa, is amply shown by the examples given. At no place has the author crossed swords with the classical taxonomists having, instead, merely analyzed the various

examples; in less patient hands they might easily have been bludgeoned over the head with what to them must surely be bitter facts.

The author tells us what genic introgression is, how it is initiated, how it operates, and what its results may be; he even presents us with an interesting and lucid chapter on various special techniques for studying and measuring it. But, as a geneticist, he has wisely refrained from recommending how such situations are to be handled nomenclaturally.

It appears quite probable, if one may look ahead, that in the not-too-distant future the present classical hierarchy of "species, subspecies, variety, and form" will be found inadequate to express with any real precision the spread of variability which is present in nature, and that a totally new system will have to be devised. What form this new nomenclatural system will take not even this reviewer is sufficiently rash to predict. However, if taxonomists are to continue naming organisms some fuctionally workable system must be devised to take proper care of the biologically important and ubiquitous phenomenon of introgressive hybridization. It is a responsibility which the taxonomist dare not evade, lest he become a dilettante member of the body biologic.

The text of this small volume is easy to read, being without the mass of interpolated (and perhaps necessary) mathematical formulae characteristic of so many present-day advanced works on population genetics. However, the mathematics of a naturally segregating population always is there, bolstering the background of the account, but never intruding sufficiently to obscure the fundamental picture of the broader aspects and implications of the situation. Therefore the busy herbarium taxonomist can offer no excuse for not reading this brief and lucidly written work. Furthermore, if he is honestly conscientious, he may be brought to ask himself just what sort of botanical data he is gathering when he hurriedly snatches a single specimen from a large and often variable local population.

The author clearly indicates that he is not dealing with such phenomena as apomixis and polyploidy; they are outside the scope of this monograph. However, the reader should disabuse himself of any idea he might have that polyploids cannot be afflicted with introgressive hybridization. To one who has to be continually dealing with such things, it is obvious throughout much of the text that the author is outlining the genetics of diploid populations. What Dr. Anderson has to say about the inherent and actual complexity of an introgressively hybridized population on the diploid level would be increased in geometric progression were he to have taken his readers through the various polyploid levels as well. Fortunately for the classical taxonomist who perhaps might be easily scared with para-astronomical numbers, as yet no precise analytical data are available regarding such populations. But the potentialities should be kept in mind by those dealing with polyploidally complicated groups.

Because of space limitations the author has had no opportunity to venture down some of the interesting byways of the problem. One of the most disconcerting things for a student is to discover that what he supposed to be only a case of introgressive hybridization actually is an instance of a segregative allopolyploid, perhaps superposed in nature on a case of true introgression on the diploid level. The close series of apparent "hybrid intergrades" found where the species involved already are polyploid and have a still higher allopolyploid population superposed on them is, to say the least, somewhat confusing to the student beginning a population analysis. Having fallen into this botanical booby-trap on various occasions in the past, this reviewer knows how embarrassing it can be. There is no way yet known to be reasonably certain of avoiding this error except by making a rapid cyto-reconnaissance of the material. If the group under scrutiny proves to be homoploid then Dr. Anderson's methods for the detection and analysis of introgressive hybridization will be effective and revealing. On the other hand, if a sampling of the group indicates the presence of a heteroploid condition, then quite a different series of analytical techniques will have to be brought to bear on the problem before it can be satisfactorily clarified.

There are several other places where this reviewer could wish that the author might have had opportunity to expand the text. One of these is in Chapter 4 where it is postu-

lated that, in a segregative population, the extreme homozygous types would tend to increase in frequency in succeeding generations, "the exact results depending on the natural mating system, the size of the populations, etc." It is hoped that "etc." covers such things as sterility factors for, in general, these tend to accumulate with the advent of homozygosity; therefore, population segments with such genetically determined sterility factors—and additional examples are being discovered all the time—usually trend more toward the heterozygous than the homozygous condition. Linkages and the "recombination spindle" admittedly do tend to keep the bulk of a segregating population with certain bounds; even so, evolution does not proceed with the norm but with the exceptional, and selective forces surely will eccentuate fortuitous nodes of accumulation on the over-all gene pattern.

There is, however, one theme running through the book with which this reviewer would take issue. This is neither a criticism of material nor of interpretation but, rather, one of a repeated implication which is bound to crystallize the reader's attention on special events, leading to a possible conclusion that introgressive hybridization is a rare and transitory phenomenon of no great importance in the broader interpretations of general systematics. Certainly the author does not say this; in fact he cautions that it is otherwise. Yet the implications from the various examples given might lead the casual reader who has done no work in genetically introgressive populations to regard the phenomenon as of sporadic occurrence. For example, on page 13 one reads that "it is only where man or catastrophic forces have 'hybridized the habitat' that any appreciable number of segregates survives"; man as the primary disturbing agent in restricted areas is the recurrent theme in Chapter 1; on page 62 we read again of "Floods, fires, tornadoes, and hurricanes" and on page 63, in times of flood "Trees are undermined and swept away; . . . plants are transported bodily"; etc., as if these were the sole factors initiating introgressive hybridization. Now this reviewer certainly does not discount them as important factors; they are real and potent. Furthermore, they are about us every day and we can easily see them in action, note their immediate effects, and observe the results on the populations moving into these catastrophically affected but often relatively restricted areas, especially since they are easily encompassed by the individual student. Yet, important as they are, they are not the only factors—perhaps not even the most important factors—upon which we should keep our eyes and attention focused. Quite often their best function is served by providing restricted areas wherein may be observed, in miniature, something similar to the development of the great genic complexes of the past out of which our present floras have developed.

On page 65 the author admits that it is "probable" that Pleistocene conditions may have had much the same effect as these lesser phenomena, and that the eastward extension of the grasslands in post-Pleistocene time also may have been an important factor in setting the stage for introgressive hybridizations in many groups. Although the advances of the Pleistocene ice-fronts certainly were catastrophic, their retreats scarcely should be classed as such—and it was during the retreats that the many new habitats were laid open for occupancy by the introgressants with their various genic combinations. The factors causing the eastward advance of the grasslands, an event that probably was initiated in the present Sonoran region as early as the Miocene and which reached its eastward maximum no more than 6,000 years ago, certainly had a deleterious effect on the forests of a wide area during the long period of that great floristic migration, but it is doubted that the movement should be thought of as coming under the heading of sudden catastrophe; certainly it would not be of the same order as a local flood, a fire or tornado.

The fluctuations and ultimate emergence of the southeastern Atlantic and Gulf coasts of America throughout the Tertiary yielded a series of different, intergrading and constantly changing habitats; earth-movements and not man initiated the changes, and they were neither sudden nor catastrophic. The present complexity of the flora in that region is both a reflection and evidence of the long series of hybrid introgressions which have been taking place there. And it is the firm conviction of this reviewer that the

present baffling complexity of the flora of the Amazonian Basin can be laid to the geologically recent emergence of parts of the area after a possible brief marine invasion; therefore, the flora of much of the Amazonian lowlands would be of comparatively recent advent and so exhibit on a grand scale what one can see, in miniature, on a cut and burned-over woodland area into which a series of introgressible species had recently migrated. In brief, what one can observe after sudden catastrophies of nature open up new series of habitats, or where man disturbs an area, are only glimpses into what has been occurring on a much larger scale ever since the world was clothed with its first green mantle. It is not the sudden and perhaps spectacular catastrophe which is important; the important thing is that it leaves in its wake a series of new habitats into which organisms can venture, there to experiment with all possible combinations within their common pool of variant genes. The area of experimentation can be small or continental in extent.

From all sides one hears the lament of those who regret the necessity of studying populations under what they term "disturbed conditions." If it were possible they should ask that pool of genes which comprises the genus *Quercus* if it knows of such a thing as a really stable habitat. Were it able to answer it could tell of many events since the breaking dawn of the Cretaceous when, already, it was a large and lusty group: it could tell of great territories foundered beneath the waves, of lands come up out of the sea, of mountain ranges that have reared their peaks into the zone of perpetual snow, of sharp crags worn down to softly contoured plains, of climatic changes in certain areas which ran the whole gamut of variability from subtropical to arctic or from rain-forest to desert, and of the waxing and waning of great groups of browsing or acorn-stealing animals. If the oak genes could talk they would say that there is no such thing as a stable habitat. Yet the oaks of today are no more and no less oaks than were their ancestors of the Cretaceous, and anyone who will bother to read the record in the rocks will see that, to keep the place they have in the world's flora in the face of widely differing and constantly changing habitats and conditions, it was often necessary to dip deeply into the common pool of basic genes with which the group was long ago endowed. The genic introgressions which we see so commonly in our modern oaks—to some a most startling and ususual series of phenomena—are probably no different either in their nature or magnitude from those which certainly must have taken place almost continually in the past. It is not the expected linear evolution of the oaks since the Cretaceous which primarily intrigues us; it is the reticulate nature of much of their post-Cretaceous evolution that astounds, a reticulum maintained throughout this long period solely by the phenomenon of introgressive hybridization.

For the taxonomist venturing for the first time from the conceptual confinement of herbarium study into an analysis of living populations in the green world outside, Dr. Anderson's little book will be a great comfort. From it he can learn much to assist him in understanding the basis and mechanics of the variability he is certain to encounter in some nearby stretch of woodland or a single meadow. From these introductory analyses he can proceed to adjacent areas; and so on, if need be, to encompass a whole continent with adequate sampling methods. First, however, let him be warned that his primary study of introgressive hybridization may be the opening of a veritable Pandora's box for, as he delves further within the secrets of the group he studies, he well may uncover such taxonomic ills as polyploidy, aneuploidy, apomixis, and other items which currently plague the workers in the new systematics. But if he be of stout heart and persistent, let him remember also that, underneath the ills, Hope lay at the bottom of Pandora's box—W. H. CAMP.

NOTE

The availability of money from the Mary S. Andrews Research Fund was announced in this journal, vol. 75, p. 585 and the grants appear in the Minutes of the meeting of April 5, 1949. The proposed uses are of wide interest. Dr. Robert Clausen of Cornell University, Ithaca, N. Y., has in mind "a taxonomic study of the genus *Sedum* in the

Sierra Madre Oriental of Mexico.'' Dr. Richard Goodwin, Connecticut College, New London, Conn., will continue ''a study of fluorescing substances in roots.'' Dr. Goodwin reported to the Club on some of his studies of these substances at the meeting of April 5. Dr. Heimsch, University of Texas, Austin, Texas, wishes to make ''comparative anatomical studies of angiospermous families.'' Brother Leon, Colegio de La Salle, Vedado, Habana, Cuba, will use his portion ''to assist in the preparation of volumes on the 'Flora de Cuba.' ''

In addition to the usual courses offered at the New York Botanical Garden this autumn there is to be one for beginners in the study of fungi. This will meet Saturday mornings, starting Sept. 17, for five weeks. Collecting and identification will be stressed with emphasis on distinguishing the poisonous from the edible forms.

INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY

LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITORS OF THE TAXONOMIC INDEX

TAXONOMY, PHYLOGENY AND FLORISTICS

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